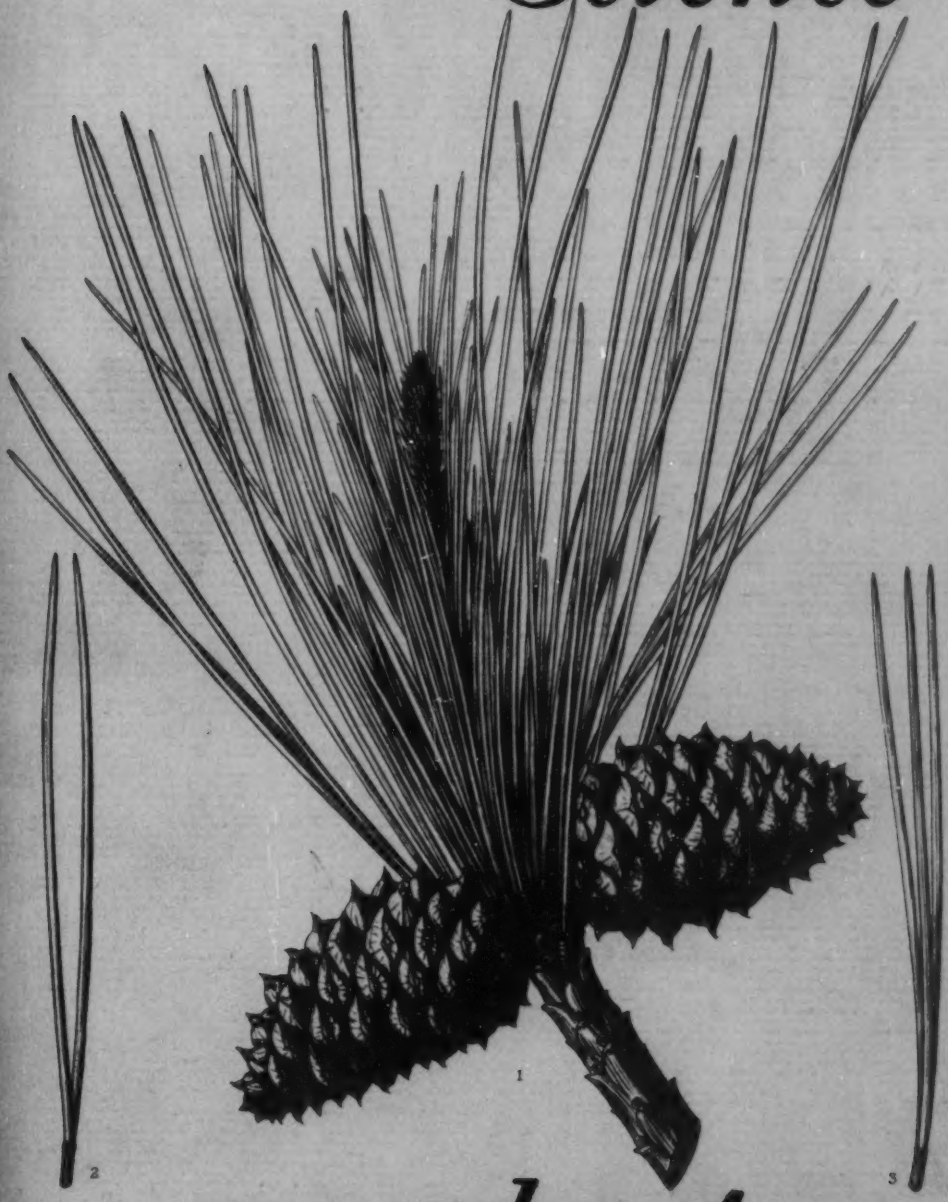
FOREST Science



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number 4

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The cover design is a reproduction of a steel engraving by Charles Edward Faxon in Sargent's *Silva of North America*, 1890-1902.

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Soil Water Depletion by Pine and Hardwood Stands During a Dry Season

BY
ROBERT ZAHNER

THORNTHWAITE (1945, 1948), Mather (1950), Stone (1952), and others have implied that, for a given climatic zone and within broad vegetative types, evapo-transpiration is independent of the specific character of plant cover. A recent study in southeastern Arkansas substantiates this theory in that the soils of two well-forested areas of different species, but similar in climate, stocking, and site, were depleted of water at approximately the same rate.

The Problem

For a given climatic condition, and in a fixed soil and topographic situation, the rate at which water is removed from the ground depends on the transpiring effectiveness of the crown canopy and upon the distribution of roots in the soil. Since the rooting habits and leaf surfaces of different species are inherently different, it might appear that a stand of broadleaf species would not transpire the same amount of water as an equivalent stand of pine.

Comparisons of transpiration among different species has in the past been limited largely to individual trees or potted seedlings. Minckler (1939), for example, measured transpiration from a number of representative branches of large forest trees. When he applied his results to forest stands, they suggested that a red maple forest might transpire more than twice as much water as a white pine forest with trees of comparable size.

Kramer (1952) points out that laboratory studies have shown that pines may transpire less rapidly than oaks, per unit of leaf area. However, he noted that this relationship might be reversed by differences in total leaf area among species.

Stone (1952) questions the effect of species differences on rates of water loss when soil moisture is not limiting. But he concedes that, after the soil has dried somewhat, differences in rooting habits are probably reflected by differences in water loss. He further points out that recent investigations by climatologists suggest that the rate of evapo-transpiration is regulated primarily by the solar radiation absorbed by a land area.

Moyle and Zahner (1954), working on the Crossett Experimental Forest in southern Arkansas, found that a young even-aged hardwood stand, an all-aged hardwood stand, and an all-aged pine stand each removed about the same amount of water from the ground over the same period of time. However, density of stocking, basal area, and understory were not uniform among the three stands studied.

The Experiment

To supplement the original work of Moyle

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and Zahner, rates of soil water depletion by forests of pure pine and of pure hardwood were measured during the summer of 1954. In this study, stand and site conditions of each forest type were kept as similar as possible.

The object was to measure the rates of soil water loss through a broad-leaved canopy and through a canopy of pine. Transpiration was not measured directly, but was assumed to be the primary agency in soil moisture depletion under the conditions studied.

Study areas. On the Crossett Experimental Forest two 50- by 50-foot plots were established in a hardwood stand and two in a pine stand. Plots were selected so that the numbers and sizes of the stems on each were as equal as possible (Table 1, Fig. 1).

The hardwood plots were in a 35-year-old even-aged, well-stocked stand of southern red oak (*Quercus falcata* Michx.), post oak (*Q. stellata* Wangenh.), and blackjack oak (*Q. marilandica* Munenchh.). The stand is being managed for the production of sawlogs, with southern red oak the favored species. One thinning for chemical wood was made 5 years ago.

The pine plots were in a 20-year-old even-aged stand of loblolly (*Pinus taeda* L.) and shortleaf (*P. echinata* Mill.) pine. The stand had originated as natural reproduction. It had been released from overtopping hardwoods at 5 years of age and lightly thinned for pulpwood at age 14.

Both the hardwood and the pine tracts had been free of any cutting for at least 5 years prior to 1954. Neither had ever been completely cleared of forest cover. The understory on both areas consisted of a sparse distribution of *Crataegus, Vaccinium,* and other shrubs. The litter had been free of disturbance by fire and excessive grazing for many years.

FIGURE 1. Left: the pure pine area. Right: the pure hardwood area.

TABLE 1. Stand data for the four study plots.[1]

Type	Plot	Stems	Basal area	Average d.b.h.	Age
		Number	*Sq. ft.*	*Inches*	*Years*
Pine	1	24	5.2	6.3	17–18
	2	26	5.6	6.3	18–20
Hardwood	1	21	5.7	7.1	35–39
	2	24	4.7	6.0	25–35

[1]Based on trees 3.6 inches d.b.h. and larger on each 50- by 50-foot plot.

Topography was of the "upland flatwoods" type, with imperfect surface drainage. The soil under all 4 plots was classified as Leshe[1] silt loam. This soil is characterized by a dark grey silt loam surface soil which grades into a yellow silt loam subsoil at from 8 to 12 inches. A pan of mottled grey-yellow silt loam exists at about 24 inches. Internal drainage is slow. Table 2 summarizes soil profile data for the 4 plots. Loblolly pine site index for Leshe soil on imperfectly drained sites is about 90 feet at age 50.

Sampling methods. Soil moisture was sampled weekly beginning on May 19 and continuing through September 8, 1954. On each sampling date, four points were located within a plot, and a hammer-driven tube sampler was employed as described by Olson and Hoover (1954). The 6- to 12-inch depth and the 36- to 42-inch depth were sampled on one pine and one hardwood plot every week and on both pine and both hardwood plots every other week. The 21- to 27-inch depth was sampled every two weeks on one pine and one hardwood plot, and every four weeks on all plots. The 54- to 60-inch depth was sampled every four weeks on one pine and one hardwood plot, and every eight weeks on all plots. No samples were taken from the surface-to-6-inch depth because the moisture content of this layer fluctuates so greatly with occasional showers.

[1]Series tentatively assigned pending correlation.

Rainfall. Rainfall was recorded daily. Gages were placed in open areas near each stand.

May rainfall was more than twice the normal of 4.14 inches. From May 27 to July 19, however, only two small showers of less than 0.30 inch each were recorded. A severe drouth was therefore felt in late June and half of July. On July 19-20, 3.17 inches fell on the hardwood area, wetting the soil to a depth of 14 inches; and 1.67 inches fell on the pine area, the water reaching a soil depth of 8 inches. Thereafter conditions were again dry, except that on August 27 1.14 inches fell on the pine area and 0.57 inch on the hardwood area.

Measurements and analyses. Moisture contents were determined gravimetrically on an oven-dry weight basis, then converted to inches of available water per 6-inch layer of soil. Available water was computed as the field moisture content minus the moisture content at wilting point.

Since the high May rainfall kept the soil at field capacity until June 2, observations prior to this date were not considered in the analysis of depletion rates.

Plotting soil moisture over time indicated that for a given depth there was no difference in rate of depletion between the two hardwood plots or between the two pine plots. Hence plot data were summarized by species and depths to facilitate comparisons between pine and hardwood.

These comparisons were made by considering depletion rates within one depth

TABLE 2. Physical properties of the soils at four depths.

Soil depth (inches)	Forest type	Composition				Bulk Density[1]	Moisture constants	
		Plot	Sand	Silt	Clay		60 cm. tension	Wilting point[2]
			Percent				*Inches of water*[3]	
6–12	Pine	1	32	52	16	1.49	1.87	0.43
		2	22	63	15	1.49	1.79	.42
	Hardwood	1	18	64	18	1.51	2.13	.53
		2	19	64	17	1.51	2.11	.49
21–27	Pine	1	30	48	22	1.55	1.97	.67
		2	22	58	20	1.56	1.93	.66
	Hardwood	1	19	57	24	1.60	2.35	.82
		2	18	59	23	1.59	2.30	.76
36–42	Pine	1	31	45	24	1.56	1.99	.81
		2	22	57	21	1.58	1.93	.78
	Hardwood	1	19	55	26	1.60	2.29	.92
		2	18	57	25	1.55	2.19	.89
54–60	Pine	1	29	49	22	1.52	.....	.72
		2	21	58	21	1.51	.....	.68
	Hardwood	1	17	59	24	1.55	.....	.84
		2	16	60	24	1.53	.....	.84

[1]Average of four replications with 250 cc. undisturbed cores.
[2]Determined at 15 atmospheres pressure in a pressure-membrane cell.
[3]Per 6-inch layer.

zone at a time. For the 21- to 27-inch depth and the 36- to 42-inch depth the observed relationships between soil moisture and time were described by fitting a function of the form

$$Y = b_0 + b_1 X + b_2 X^2$$

In this formula Y is inches of available water per 6-inch layer of soil and X is the number of weeks after the beginning of depletion.

The parabolic function was selected because it simplified comparison of depletion rates, was easy to calculate, and fitted the data closely. Its use does not imply that this type of function expresses the true relationship between moisture depletion and time. After these functions had been fitted, the species depletion rates were compared statistically by an analysis of the regression coefficients.

The above technique was not used for either the 6- to 12-inch or the 54- to 60-inch depths. In the 6- to 12-inch depth the depletion trend was interrupted by the rain of July 19-20. For the 54- to 60-inch depth the sampling system employed did not provide enough observations to warrant statistical treatment of the data. For both of these depths only visual comparison of eye-fitted curves was attempted.

Results

Species. For the 21- to 27-inch and the 36- to 42-inch depths there was no significant difference between species in the rate of soil-moisture depletion over the 14-week period. Though not subject to rigid analysis, the data indicate that similar trends exist in the 6- to 12-inch and the 54- to 60-inch layers.

A very obvious feature of the data is that the depletion curves for the hardwood stands do not coincide with those for the pine (Fig. 2). The lack of coincidence is due to differences in storage capacity arising from inherent differences in soil tex-

ture and structure. Because of their greater storage capacity, the soils under the hardwood stands lagged about one week behind the pine soils in stage of moisture depletion. The difference in storage capacity did not affect the rate of depletion, but it did cause the depletion curve for the pine sites to level off (near the wilting point) one week earlier than the hardwood curve.

Depths. On the assumption of equal rates of depletion for the two species, the data were combined to provide a single depletion equation for each depth. The one-week lag in depletion of the hardwood sites was removed by substituting $(X + 1)$ for (X) in the pine data. The combined equations for the various depths are as follows (Y = inches of available water per 6-inch layer; X = number of weeks after start of depletion):

(1) 6- to 12-inch layer
$$Y = 1.70 - 0.356X + 0.0188X^2$$
(2) 21- 27-inch layer
$$Y = 1.61 - 0.243X + 0.0093X^2$$
(3) 36- to 41-inch layer
$$Y = 1.32 - 0.173X + 0.0057X^2$$
(4) 54- to 60-inch layer
$$Y = 1.06 - 0.138X + 0.0062X^2$$

In Figure 3, points calculated by these equations have been plotted to indicate the total water loss at a given depth at a given time after the start of depletion. The depths below 3 feet lost water at about half the rate of the surface depths. However, all depths were reduced to, or near, wilting point during the study. The 6- to 12-inch depth was near wilting point by mid-July and the lower depths by mid-August.

Hoover, Olson, and Greene (1953) reported that an 11-year-old loblolly pine plantation in South Carolina removed water from a depth of 54 to 66 inches at about the same rate as from shallower depths. This plantation, however, was on a well-drained Piedmont soil, where aeration was evidently not so limiting to root growth as it is in the Leshe soil at Crossett. Aeration in Leshe soil is poor during periods of excess water in spring, and tree roots are not extensively developed in and below the silt loam pan.

Aldrich, Work, and Lewis (1935) reported correlations between relative root concentration and moisture extraction from corresponding depths on a poorly aerated heavy clay soil. Roots of pear trees removed twice as much water from the sur-

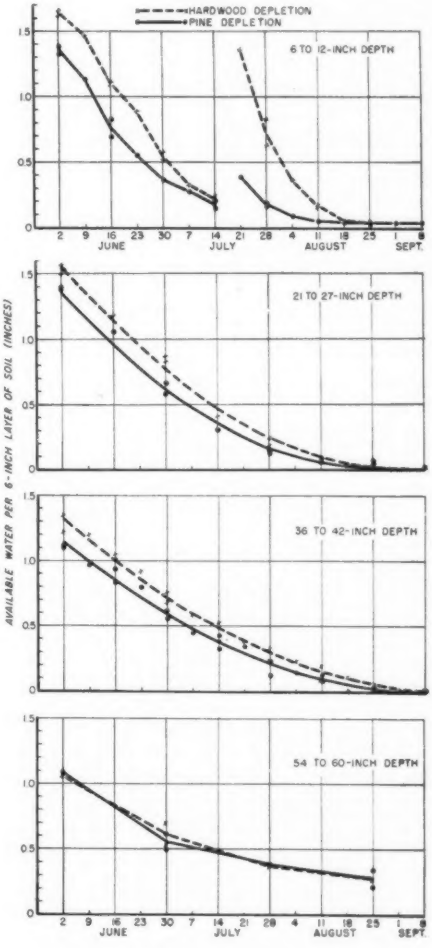

FIGURE 2. Soil-moisture depletion from pine and hardwood stands. Each plotted point is average of four field observations.

face foot of soil as from the 3- to 4-foot layer.

Because of the progressively fewer roots with depth, the additional water in the lower layers in July may have been largely unavailable to the trees. As Kramer (1949) points out, soil in contact with tree roots may be at wilting point, while soil at the same depth but a few centimeters away from roots will remain near field capacity. Sampling such a soil would yield an average moisture content well above wilting point. In the present study, the trend of the 6- to 12-inch layer was perhaps more indicative of the availability of water in the whole profile than the depletion rates at the lower depths would lead one to believe.

Total depletion. By means of equations (1) through (3), it was estimated that the water loss from the upper 48 inches of soil in either the pine or hardwood stand was about 0.19 inch per day for the 6-week period following June 2. This rate is almost identical to the estimate of 0.20 inch made by Moyle and Zahner (1954) for forested areas on similar sites for the same period in 1953.

The total loss of moisture from the entire profile is estimated to have been about 0.25 inch per day for the first 6 weeks of the study. This estimate is based on the assumptions that equation (4) represents the depletion from the soil layer between 48 and 66 inches and that half this rate prevailed from 66 to 72 inches. Depletion below 6 feet was considered to be negligible in the soil type under study.

Potential evapo-transpiration. Mather (1950) defines potential evapo-transpiration as the amount of water that will be lost from a land surface completely covered with vegetation if there is sufficient water in the soil at all times for the use of the vegetation. Calculations of the potential evapo-transpiration (Thornthwaite, 1948) for the Crossett area[2] give a value of something less than 0.22 inch of water daily for June and July 1954. The closeness of this value to the initial rate of depletion obtained in the present study hints that even soil and topography have little bearing on evapo-transpiration within the same climatic area when the soil is moist.

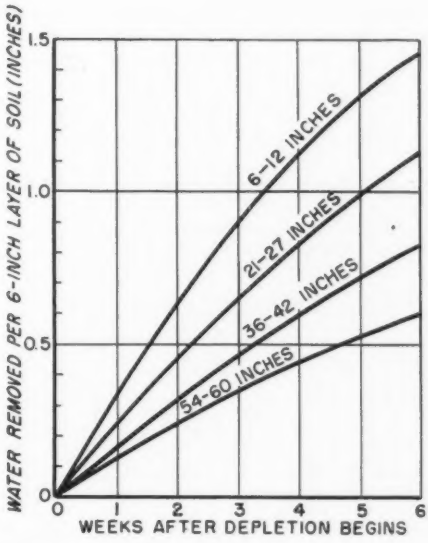

FIGURE 3. Initial 6 weeks of water losses from the four depths sampled.

Summary

A study in southern Arkansas measured the depletion of soil water by even-aged stands of upland oaks and of loblolly-shortleaf pine. Stand and site conditions were similar for both species groups. Four soil depths to 60 inches were periodically sampled during the hot, dry summer of 1954.

Data indicated little difference in rate of loss between the two stands for corresponding depths.

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[2]Thornthwaite's equation for potential evapo-transpiration is based on a heat index calculated from mean monthly temperatures and corrected for the length of day of the period under consideration.

Between depths there were marked differences independent of species. In both stands, layers below 3 feet lost water at about half the rate of the upper layers.

For the 6 weeks beginning June 2, the rate of loss for both forest types was about 0.19 inch per day from the upper 4 feet of soil. This rate coincides with that previously reported from well-stocked all-aged hardwood and pine stands on similar sites.

The estimated initial loss of 0.25 inch per day from the entire soil profile agrees closely with the potential evapo-transpiration for the Crossett area as calculated from Thornthwaite's formula. These agreements support theories that evapotranspiration within a given climatic area is independent of the type of forest cover.

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Moisture Content of Oaks and Mat Formation by the Oak Wilt Fungus

BY
ROBERT N. CAMPBELL
DAVID W. FRENCH

Endoconidiophora fagacearum Bretz, the cause of oak wilt, forms spores on mycelial mats under the bark of wilted trees (Curl *et al.*, 1953). These mats split the bark and thus liberate the spores (Leach *et al.*, 1952). Hepting (1955) reviews the evidence that insects of the Nitidulidae or sap beetle family frequent these mats and are mainly responsible for carrying spores to fresh, bleeding wounds in the spring. These mats are the most important and probably the only source of inoculum for overland spread of the pathogen.

The purpose of the present study was to trace the moisture content of oak sapwood from the time the tree wilted until the mycelial mats were formed and thus determine the relation between host moisture content and mat formation.

Fergus (1953) in Pennsylvania found that the moisture content of the sapwood of freshly wilted oak trees averaged 49.5 percent while that of trees on which *E. fagacearum* was forming mats averaged 42.5 percent and ranged from 37.5 to 48.4 percent. Only 3 trees in each of these 2 categories were sampled. He suggested that the fungus was stimulated to mat formation by the reduction of moisture content in the sapwood which increased available oxygen for the fungus.

Materials and Methods

The trees in this study were northern pin oak, *Quercus ellipsoidalis* E. J. Hill, growing in the vicintiy of St. Paul, Minnesota. These trees ranged from 3 to 9 inches d.b.h. In the early part of this study the wilting and mat-bearing trees were naturally infected. Beginning in June, 1954, diseased trees were those which had been inoculated during the winter of 1953-54. These trees were inoculated with a concentrated spore suspension injected into the butt of the tree.

When sampling for moisture content, the trees were felled and the limbs removed immediately to reduce any loss from transpiration. Disks were cut from healthy trees at 1½ and 5 feet above the ground and every 5 feet thereafter to a top diameter of 1½ to 3 inches. The same method was used for diseased trees, except that when mats were present, disks were cut through them and at 5 foot intervals to the top.

The disks were about 1½ inches thick. Two pairs of sapwood and outer heartwood samples were taken from opposite sides of

---

Campbell and French are respectively instructor and assistant professor, Department of Plant Pathology and Botany, Institute of Agriculture, University of Minnesota, St. Paul.

Supported in part by grants from the National Oak Wilt Research Committee. The authors wish to express their appreciation for the statistical advice given by Dr. H. L. Thomas, Department of Agronomy and Plant Genetics, University of Minnesota. Paper No. 3434, Scientific Journal Series, Minnesota Agriculturial Experiment Station.

TABLE 1. The average moisture contents (percentage on wet weight basis) of sapwood and heartwood of healthy northern pin oaks in different stages of growth.

Tree No.	Tree Condition: Dormant Sapwood	Dormant Heartwood	Budding Sapwood	Budding Heartwood	Growing Sapwood	Growing Heartwood	Resting Sapwood	Resting Heartwood
				Percent				
1	40.7	47.6	41.0	42.6	44.0	43.5	39.8	45.0
2	43.6	46.4	40.0	44.7	47.3	46.2	42.7	44.0
3	42.5	49.0	40.3	44.0	44.3	44.4	42.6	46.2
4	40.0	44.9	42.6	45.2	46.1	49.5	40.9	46.2
5	38.8	46.0	40.0	41.8	46.3	46.1	41.0	45.2
6	38.3	42.4	40.8	44.1			38.1	45.6
7	39.0	45.6					40.4	46.1
8	37.6	42.1						
9	40.1	42.7						
10	37.6	43.7						
11	39.5	43.4						
12	39.5	43.6						
13	37.7	41.7						
Mean	39.61	44.55	40.78	43.73	45.60	45.94	40.78	45.47

Analysis of variance for sapwood moisture content of healthy trees

Source	Degrees of freedom	Mean Square	F	F at 1% level
Between averages for each tree condition	3	381.58	25.42	4.60
Between trees within each tree condition	27	15.01	8.63	1.88
Between samples within trees	249	1.74		
Total	279			

each disk. The sapwood sample consisted of the entire sapwood for about 2 inches of the circumference of the disk or enough to give a sample weighing at least 20 grams. If a sample was taken from under a mat, all surface growth of the fungus was scraped off first. A sample of about the same size was taken from the underlying heartwood. In this paper, outer heartwood moisture content is referred to as heartwood moisture content.

As soon as a sample was chipped from the disk, it was placed in a seamless tin box. On returning to the laboratory, the cans were weighed to within 0.01 gram. The rate of water loss from these cans during transit was found to be much less than 0.01 gram per hour. The samples were oven dried to constant weight at 105°C and reweighed. The moisture contents were calculated on the basis of the wet weight of the wood. These can be converted to oven-dry basis graphically (McMillen, 1950).

The radial thickness of the sapwood of these trees ranged from $\frac{3}{16}$ to $\frac{3}{4}$ inch with most of them in the range from $\frac{1}{4}$ to $\frac{1}{2}$ inch. The number of annual rings included in the sapwood varied from 2 to 9 but most of the trees had from 3 to 5 rings.

Seasonal Changes in Sapwood Moisture Content

The moisture contents of 31 healthy trees have been determined, representing all phases of growth (Table 1). The sapwood moisture content within a given tree was constant throughout the length of the bole; there was no gradient from top to bottom.

TABLE 2. The average moisture contents (percentage on wet weight basis) of sapwood and heartwood of oaks in different stages of wilt and mat formation as compared to condition of healthy trees at time of sampling.

Condition of healthy trees at time diseased trees were cut	Condition of diseased trees									
	Wilting		Mat-bearing-fall		Mat-bearing-spring					
					Mat zone		Above mat zone		Past mats	
	Sapwood	Heartwood	Sapwood	Heartwood	Sapwood	Heartwood	Sapwood	Heartwood	Sapwood	Heartwood
	Percent									
Growing	45.6	44.5								
	48.6	48.5								
	46.2	45.5								
	48.6	46.0								
	46.4	45.9								
	46.4	44.5								
	44.8	40.3								
	50.2	49.3								
	48.7	47.7								
Resting,	45.5	44.6	45.2	46.6	41.6	47.0	39.4	46.0	28.6	38.4
Dormant, or	45.5	44.5	51.4	49.3	43.5	46.6	40.4	44.7	34.8	42.8
Budding			46.6	45.9	42.0	46.9	29.8	45.7		
			47.9	44.4	37.4	44.9	29.4	39.6		
			48.5	49.0	40.5	45.7	32.3	42.4		
			44.5	46.9						
			45.9	43.7						
			46.0	45.6						
			46.5	47.0						
			46.9	44.4						
			45.1	42.8						
Mean	46.95	45.57	46.77	45.96	41.00	46.22	34.26	43.77	31.70	40.60

Analysis of variance for sapwood moisture content of diseased trees

Source	Degrees of freedom	Mean Square	F	F at 1% level
Between averages for diseased condition	4	2,281.51	31.62	4.04
Between trees within diseased condition	29	72.15	4.96	1.76
Between samples within individual trees	333	14.53		
Total	366			

The dormant trees were sampled in late fall after the leaves had fallen and during the winter. Trees that were budding out were sampled from May 13 through May 20, 1954, and from April 26 through April 30, 1955. It is not known whether radial growth had begun at these times; however, the bark slipped easily, indicating that cambial activity had begun. The growing trees, sampled from June 15 to July 20, 1954, were considered to be growing radially because they were in full leaf, the current annual ring did not appear complete, and the bark still slipped easily. Trees in the resting condition were those sampled after July 29, 1954, and before leaf fall. During this time, although the leaves were green, the bark did not slip and the annual ring appeared to be complete.

A statistical analysis of the sapwood of these healthy trees showed a significant difference between the tree condition classes (Table 1). The difference between the sapwood moisture content of growing trees and that of each of the other classes was shown by a *t* test to be highly significant.

The significant differences shown within groups could have arisen from genetic variation between trees or differences in site, or both. The variance between trees within each tree condition group (15.01, Table 1) is an estimate of the sampling variation which must be reckoned with in comparing averages of condition groups.

Effect of Oak Wilt on Sapwood Moisture Content

The moisture contents of 29 trees that were wilting or were in various stages of mat formation were determined (Table 2). The condition of comparable healthy trees at the same time is indicated. The mat-bearing trees were of 2 types: those bearing mats during the fall of the year they wilted, and those bearing mats in the spring after wilting late the previous summer (Campbell and French, 1955). The samples from trees in the latter group were divided into those coming from the lower portion of the bole where mats were being produced at the time of sampling and those coming from above this mat zone. The two trees which were past mat production were cut and sampled eight months after mats had been produced.

An analysis of variance for the data in Table 2 indicated significant differences between the sapwood moisture content of trees in different diseased conditions. There was no difference between wilting trees and those bearing mats in the fall. The moisture content of the mat-zone of trees bearing mats in the spring was shown by a t test to be significantly lower than that of trees bearing mats in the fall. When trees overwinter in the wilted condition, there is a significant decrease in moisture content even in the lower portion of the bole where the fungus forms mats the following spring.

Comparing the data from diseased trees to those from healthy trees (Table 1), it will be seen that the moisture content of the sapwood remains high when the tree wilts and bears mats in the same season. A t test showed no significant difference between sapwood moisture content of growing, healthy trees (45.60 percent, Table 1) and trees bearing mats in the fall (46.77 percent, Table 2).

The 68 sapwood samples taken directly under fresh, young to mature mats had an average moisture content of 47.6 percent with a range from 43.7 to 53.2 percent. The moisture content of the heartwood samples from these trees averaged 46.6 percent and ranged from 33.9 to 53.6 percent. These figures are for trees on which mats were borne the same season as wilting occurred.

Seventeen samples were taken directly under the fresh mats on trees that were producing mats the spring following wilt. The sapwood samples averaged 41.4 percent and ranged from 37.2 to 45.0 percent. The heartwood samples averaged 46.3 percent and ranged from 44.9 to 47.8 percent.

When comparing the trees of different sizes it was noted that the smaller trees wilted and passed through the mat-bearing stage much more rapidly than did the larger trees. Also in larger trees the moisture content was more variable since the top began to dry out while mats were being formed on lower parts of the bole. No difference was noted between mat-bearing trees that were naturally infected through root grafts and those that were inoculated artificially.

Discussion

Although seasonal changes in the moisture content of wood have been investigated for other tree species, no work appears to have been done on any oak species. Due to the limited extent of this study, the effect of different tree sizes and stand conditions on oak moisture content were not determined. It has been shown that for part of the year the sapwood moisture content was much higher than during the remainder of the year, and was approximately equal to that of the heartwood. In 1954 this period of high sapwood moisture content extended from before June 15 to between July 20 and 29.

High sapwood moisture content appears to be directly related to cambial activity and the formation of current annual wood, when the tree is fully leafed out. The observation that radial growth ceases long before leaf fall is supported by dendrometer studies on other oak species (Daubenmire and Deters, 1947; Eggler, 1955; Fraser, personal correspondence, 1955). It has been shown that cambial activity generally begins when the leaves are developing (Daubenmire and Deters, 1947; Eggler, 1955). It is not known why the sapwood moisture contents were not higher during budding-out since cambial activity was observed then.

The effect of oak wilt on host moisture content and the subsequent effect of host moisture content on mat formation by the pathogen seems to be clearly defined. When a tree wilts, the moisture content of the sapwood remains for some time at a level near that prevailing when the tree is growing. Most wilting is observed during this period. The continued high moisture content probably is due to plugging of the vessels by tyloses and gums (Struckmeyer *et al.*, 1954) and the subsequent reduction in water flow (Beckman *et al.*, 1953). The fungus then forms mats while the sapwood moisture content is high.

As a result of this experiment and additional observations on the behavior of the fungus it is postulated that for optimum mat production the pathogen requires, among other things, a high sapwood moisture content. This is found in trees wilting and reaching the mat-bearing stage in the same year. Less favorable host moisture conditions are found in trees which do not reach the mat-producing stage until the spring following wilt due to dessication during the winter.

The fact that host moisture content would normally be at low levels when trees wilt in September (Table 1), and that drying out occurs in wilted trees during the winter could explain, in conjunction with unfavorable seasonal temperatures, the poor mat formation observed on trees that wilted in September (Campbell and French, 1955).

Most of the emphasis in this study has been on the sapwood since it has been found that the fungus is limited to the sapwood. Young (1949) found the fungus restricted to the outer ¼ inch of sapwood and Henry and Riker (1947) found the fungus extending into 2-year-old summerwood. Although only the outer heartwood was sampled, the results are close to the 47 percent given for the entire heartwood (Peck, 1948).

Mat formation has been reduced or eliminated by felling or deep girdling (Boyce, 1954; Morris, 1955). This may be due to the reduction of the moisture content below that suitable for mat formation before the trees reach the mat-producing stage. It has been pointed out that girdling as a means of reducing water content is effective only if a complete ring of sapwood is removed (Gibbs, 1939).

Summary

During the period from October, 1953, through April, 1955, the moisture contents of 60 healthy and oak wilt-infected northern pin oaks were determined in Minnesota.

There was a seasonal fluctuation in the moisture content of the sapwood of healthy trees. During the period of radial growth the moisture content averaged 45.6 percent (wet weight basis), which was approximately equal to the year-round averages obtained from the outer heartwood. During the remainder of the year, when the trees were in the rest period, dormant, or budding-out, the sapwood moisture content was about 40 percent.

The sapwood moisture content of wilted trees was at the high level of radially growing trees. It remained at this level when mats were formed the same year as wilt occurred. However, when mats were not formed on the wilted trees until the following spring, the moisture content near the mats had dropped to 41 percent. The mois-

ture content averaged 31.8 percent on 2 trees that had passed through the mat-forming stage 8 months previously. The moisture content of the sapwood under fresh, young to mature mats ranged from 43.7 to 53.2 percent in fall and from 37.2 to 45.0 percent in the spring.

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A New Dendrograph for Recording Radial Changes of a Tree

BY
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EDWIN C. FRITTS

THE ANNUAL INCREMENT in trees has been used by foresters, ecologists, and climatologists for many years. Instruments for the measurement of cambial growth, however, were not developed until 1905. MacDougal (1921) describes several of these early instruments, as well as a continuous recording dendrograph which he himself developed. The essential feature of his instrument is a floating frame which extends around a tree, contacting the bark on opposite sides. Variations in the distance between the points of contact are magnified and recorded on a clock-driven drum.

In 1932 Reineke introduced a precision dendrometer for measuring variations in radii of trees. Daubenmire in 1945 described an adaptation of the precision dendrometer. Three screws were inserted into the xylem, and by placing a specially mounted dial gauge indicator on the heads of these screws, the position of the bark with respect to the screws could be measured. Changes in this position with time gave an index of growth.

Both of these instruments have been valuable tools for tree growth studies. With the MacDougal dendrograph a continuous record of tree growth could be made and diurnal fluctuations observed as well as the yearly regimens. The Daubenmire dendrometer, however, was inexpensive, easy to install, and could be used on a large number of trees.

In 1953 the present writer found that dendrometer measurements made at three-day intervals were not completely satisfactory for careful comparisons between individual trees. Variations in successive readings of as much as 8 percent of the total year's growth made difficult comparison of results. This was probably due to both negative diurnal changes and to slight differences in placement of the instrument on the tree. Otherwise, these readings gave every indication of being precise, and had it been possible to make a continuous reading, a very accurate record of the changes in diameter, both positive and negative, in all probability would have been possible.

The MacDougal instrument had a magnification of 22 which is rather small for use on the slower growing hardwoods. It appeared to be unduly complicated and hence expensive and was difficult to mount and protect in position on a tree.

In an effort to meet these limitations the author designed and built a new instrument during the fall of 1953. It was, in essence, the incorporation of a precise recording mechanism in the dendrometer mounting mentioned above.

Contribution from the Department of Botany, Ohio State University, Columbus, Ohio, Paper No. 570.

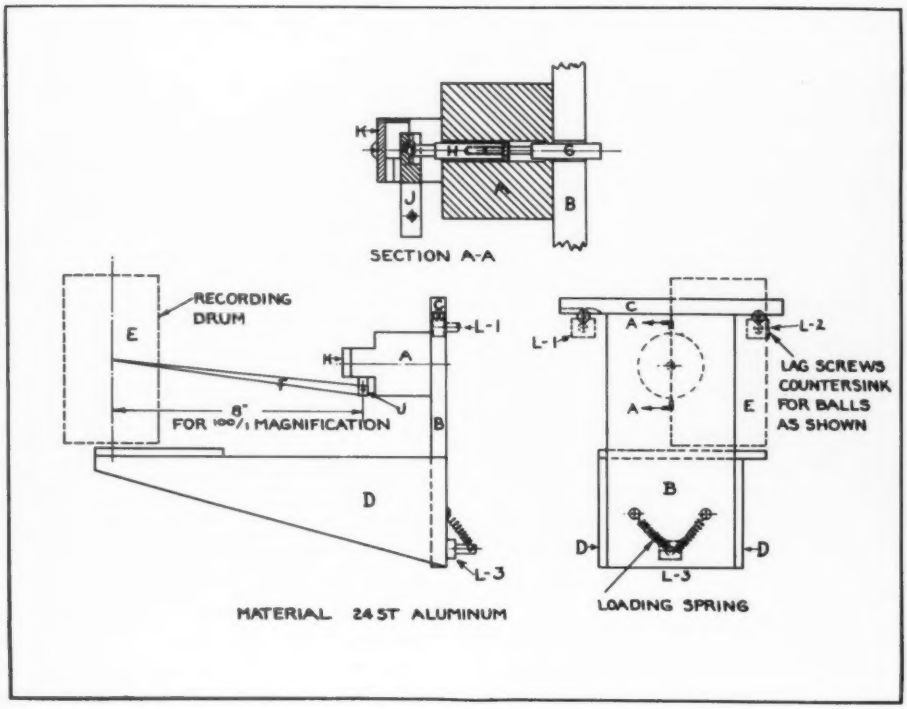

FIGURE 1. An elevation of the dendrograph.

Description

The dendrograph (Figs. 1, 2) is constructed entirely of aluminum. It occupies a space 10½ × 6 × 12¾ inches and weighs approximately seven pounds.

The principle of kinematic mounting is used in supporting the instrument on three lag screws driven into the xylem of the tree which serve as the frame of reference for the measurements. One screw (L-2) engages the frame of the instrument through a steel ball held between conical holes in both the screw and bar (C). This locates one point of mounting but permits complete freedom in rotation. A second screw (L-1) with a conical hole engages a second ball which rides in a V slot in the bar (C). This limits the movement of the instrument to a rotation around a single axis connecting the centers of the two balls. Such rotation however, is limited by a third lag screw (L-3) which engages the face of the frame (B). This mounting locates the instrument precisely without introducing spurious stresses. A loading spring holds the bar (C) tightly on the steel balls.

A similar mounting is applied to the lever system (J, Section A-A) which multiplies a hundred fold the movement of a rod (G, H, Section A-A) bearing on a prepared surface of the bark. A recording pen on the output arm (F) of this lever system marks a record on the chart for an 8-day rain gauge clock. The total arc of the pen on the chart covers 0.05 inches of movement in the rod (G, H). The small divisions of the chart (Fig. 3) represent 0.0005 inches. The rod is made of two parts (G and H), mated in a threaded section to provide an adjustment in length. Thus the instrument can easily be re-set when the pen reaches the top of the drum.

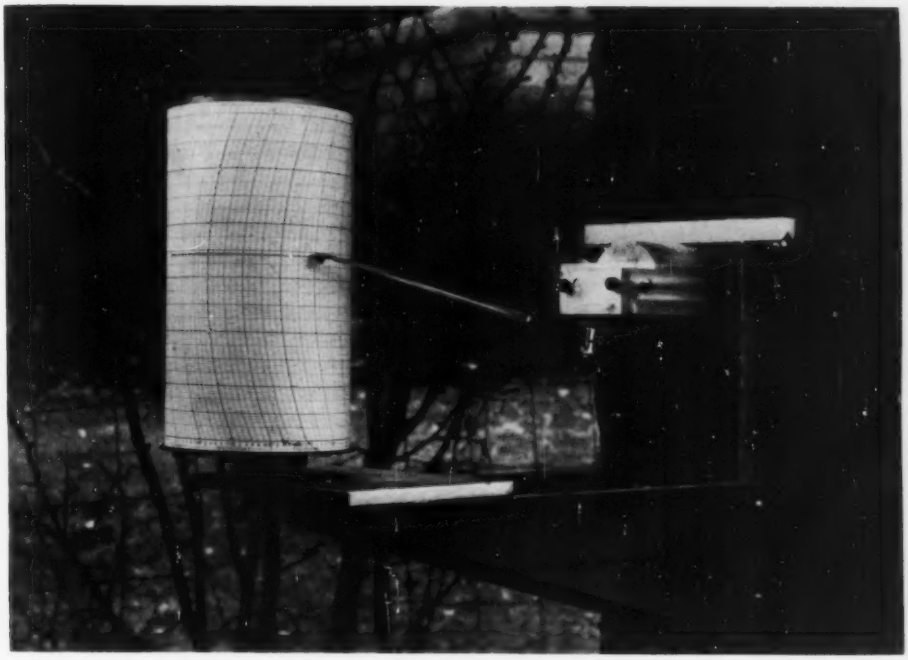

FIGURE 2. The dendrograph mounted without the protective shelter.

A nut locks G and H at the desired length. Two screws, not shown, in front of the lever (J) limit the clearance around the balls. This prevents the balls from falling out when the dendrograph is disturbed. The lever system may be disassembled by removing plate K.

Since the instrument is made entirely of aluminum, there can be no differential in thermal expansion. The lag screws, however, have a thermal expansion of approximately one half that of aluminum. But the length of the screw to the anchoring point in the tree is roughly twice the distance that the rod (G) extends beyond B in making contact with the bark. Therefore, what little differential in expansion exists in the mounting will be balanced by the length of these elements. This thermal stability has been demonstrated by an experimental check in the field.

The instrument can be sheltered in a weather-proof box strapped on the tree. In this way the instrument is securely locked and safe from biotic disturbance and weather damage.

Since the instrument does not require expensive materials, the cost is reduced below that of the MacDougal instrument. This new dendrograph can be machined and assembled for a cost of $130 not including the rain-gauge clock.[1]

Results and Applications

The dendrograph has been used in a number of locations. During the winter of 1953-54 one instrument was mounted on a Hackberry, *Celtus occidentalis* L. (Fig. 2),

[1]Manufactured by special arrangement through the author.

and during the winter of 1954-55 three instruments were mounted on Beech, *Fagus grandifolia* Ehrh. The records made by the instruments were nearly horizontal lines for air temperatures above freezing, but for lower temperatures, especially those below 25° F., a corresponding shrinkage as great as 0.013 inches was recorded. During one of these cold periods a second instrument was mounted on a metal plate and put in a near-by thermograph shelter. Even with a range of temperature from 18° to 57° F., this instrument recorded a straight line ± 0.00025 inches.

During the growing season of 1954 six instruments were mounted upon six beech trees, and all have provided reliable and accurate records of changes in radius as small as 0.0001 inch. Figure 3 is a facsimile of three weekly charts made by one of these instruments. The top chart was recorded during the early growing period when the soil moisture was high and growth rapid. Daily fluctuations at this time were at a minimum. By early June (middle chart) the soil moisture had decreased and evaporation increased so that larger diurnal fluctuations were apparent, and the daily growth increment was diminishing. On the lowest chart the trunk shrinkage became greatest on the day marked Tuesday, when the temperature rose to an unusual 104° F. and the evaporation potential was high. During the evening there was a heavy thunderstorm which replenished soil moisture, and as a result, the shrinkage on the following day was much less. This illustrates the sensitiveness of measurements to soil moisture and evaporation from day to day.

Friesner (1943) in his discussion of tree growth points out that "Hourly variations in diameter are recorded by the dendrograph (MacDougal's) during some parts of the vegetative season for all species studied. These daily reversible variations are entirely due to turgidity changes and set in whenever the transpiration loss exceeds the ability of the absorbing and conducting organs to supply water." MacDougal (1938) has demonstrated a very close relationship between diameter of trees and available moisture in his irrigation experiments.

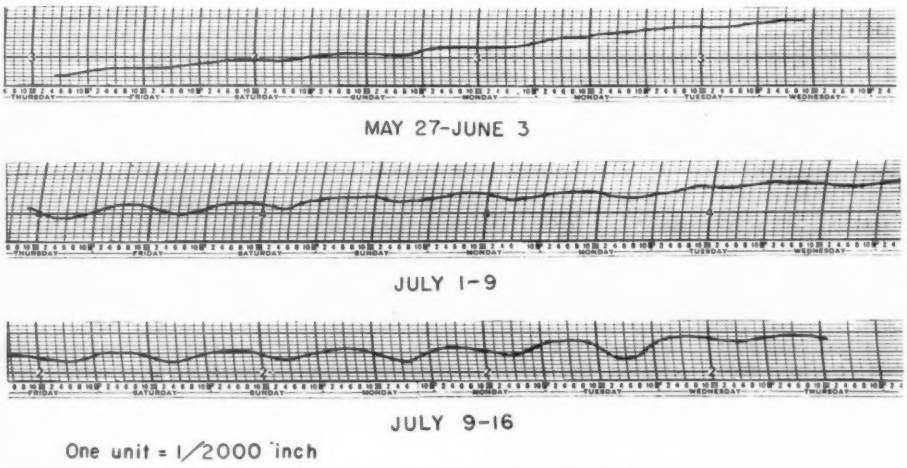

FIGURE 3. Three records made by the dendrograph on a beech tree during 1954.

The daily range in size of the tree recorded in Figure 3 is plotted in Figure 4 for the growing season of 1954. Each bar represents the maximum and minimum size of the radius during that day. Where the bars do not overlap no shrinkage occurred as in the upper chart of Figure 3, and where the bars overlap (early July) diurnal fluctuations were recorded as in the lower chart of Figure 3. From this kind of graph one can precisely ascertain both the accumulative growth curve and the magnitude of daily reversible variations (i.e. the internal water relations or turgidity changes). It is readily noted from the graph that as the reversible variations increase in late June and early July, the growth rate decreases.

The precision of the instrument was born out by a comparison of daily range in size recorded for all six trees throughout the growing season of 1954. The relative differences in growth rate from day to day were similar for all the trees. Optimum growth conditions resulted in a rapid increase while poor growing conditions were accompanied by little increase. In the latter part of the season when soil moisture became low and evaporation high, all instruments recorded similar reversible variations reflecting the turgidity changes within the tree. These also could be highly correlated with daily weather conditions.

The influence of different microenvironments however, were also evident. Instruments on trees in the better drained sites recorded a shorter growing season than those in poorly drained sites. Trees between these extremes had intermediate growth curves. Reversible variations were more pronounced in the better drained sites and generally increased as the soil moisture decreased.

The possibilities for this type of measurement are numerous. In addition to recording the reversible variations one can precisely ascertain the time of growth initiation, the daily growth increment, the shape

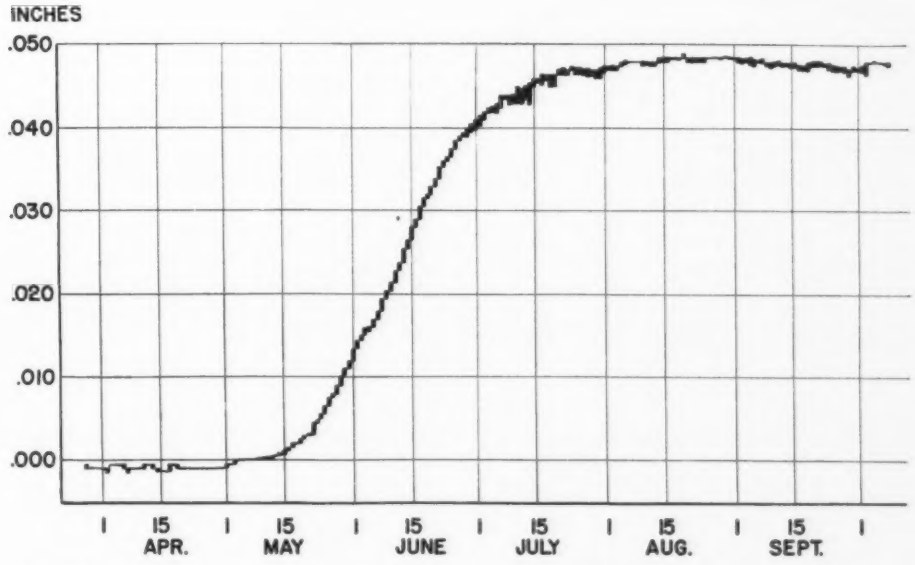

FIGURE 4. The daily range in one radius of a beech during the growing season of 1954.

of the growth curve, and cessation of growth on an individual tree and yet visit the area only once a week. Equivalent measurements with the dendrometer would entail so much time as to be impracticable, especially when the study area is not easily accessible. The dendrometer under the most favorable conditions cannot reliably measure changes less than 0.0005 inch, while the dendrograph can record changes as small as 0.0001 inch.

The precision of this dendrograph is especially valuable for microenvironmental studies where small differences in site must be evaluated. On level topography where the evaporation potential on a given day is essentially the same for all canopy trees, the diurnal variations as measured by the dendrograph can be used for directly ascertaining the relative availability of soil moisture in different sites. In areas of different exposure, however, where both evaporation and soil moisture are variables, the dendrograph records the resultant of these two factors (Friesner, 1943). The dendrograph can thus be used to ascertain the time and extent of water deficits in trees. It provides a means of rapidly analyzing the environment using the tree as an indicator. It is in this, after all, that the forester is most interested. For this reason the dendrograph should find use in a wide range of problems dealing with the forest environment. It provides in effect a unique, combined record of both growth and the influence of the total environment upon the water relations of the tree.

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Zur Frage der Steurreform in der Forstwirtschaft
(On the question of tax reform in forestry). By Hans Ostwald, Forstmeister, Geildorf/ Württemberg. 1954. Available from the author. 5.50 DM. 98 pp.

REVIEW by R. Markus

Norfolk, Virginia

This book was promoted by the newly founded (1950) German Forest Council whose president in his inaugural speech stated that forestry will be able to fulfill its economic obligations only if tax policy takes into consideration the peculiarities of forest property.

In the preamble, the author points out that the present German tax policy is detrimental to forestry in that it tends to promote a reduction in the productive capacity of the forest. He (a nephew of Dr. E. Ostwald) demonstrates how a consistent method of taxation can be developed if based on the ideas of E. Ostwald's relative forest rent theory. Utilizing relative values of forest product grades which have proved to be constant, he derives the forest capital value and from this also the forest rent which proves to be practically independent of the applied interest rate.

He recommends that only the net value of the rent should be subject to income tax whereas the balance, if any, between the annual cut and the rent is a capital gain and should be treated as such. The relative value of the rent is converted to its real value by means of the ratio between the actual market prices and the assumed relative values of the leading grades. From this rent is derived the taxable property value by applying the official capitalization interest rate.

Radiation, Surface Temperature, and Seedling Survival

BY
WILLIAM P. MAGUIRE

ACCORDING to an authority in the science of microclimatology more thought should be given to the study of surface soil temperatures (Geiger 1950). Silviculturists have stated its importance on forest seedling survival, and forest nurserymen are aware of its lethal effects on young forest seedlings.

Lethal temperatures for seedlings depend upon both the intensity and duration of the temperature (Baker 1929, Lorenz 1939). The greatest intensity of temperature occurs at the soil surface and drops rapidly both below and above this surface plane. Geiger (1950) reported a drop of 10 degrees Centigrade at a distance of one-tenth of a millimeter above the surface, and Mirov[1] has reported sub-surface temperatures which were 28 degrees C. lower than the surface temperature at an approximate depth of three millimeters.

The effect of sustained high temperatures on the biological processes of seedlings is profound, because as the temperature increases in an arithmetic progression the duration of time required to kill seedlings decreases approximately in a geometrical progression (Bigelow 1921). For example: Microscopic sections of cortical parenchyma of three-year old *Pinus strobus* L., in a water bath were completely killed in one minute at a temperature of 67 degrees C.; in five minutes at 62 degrees, and in twenty minutes at 59 degrees (Lorenz 1939).

The relationship between surface soil temperature and internal stem temperatures of seedlings does not appear to have been well established. It appears to vary with species, and age and stem-diameter are important. Baker (1929) determined that sand surface soil temperatures of 147° to 152° Fahrenheit generally were lethal to young conifer seedlings under laboratory conditions.

Daylight surface soil temperatures are principally the result of radiant energy received directly from the sun or indirectly from the sky. In this paper, the first part of the problem is the computation of the clear-sky solar and sky radiation values. These values will be related to surface soil temperatures as recorded by a Foxboro soil thermograph for certain select days (which will be described later). The ultimate goal of the study is to determine at what elevations, slopes and aspects of surfaces seedlings may be planted with reasonable assurance of satisfactory survival; and in those

[1]Mirov, N. T.-1939. Climatological observations at the Inst. For. Genetics, Placerville, Calif. 1929-1937. Unpublished.

The author is Service Forester, California Division of Forestry, at Placerville, Calif. Acknowledgment is due to the following reviewers who so kindly made comments and criticisms of the original manuscript: Dr. David M. Smith and Dr. Wm. E. Reifsnyder of the Yale School of Forestry, and T. H. MacDonald of the U. S. Weather Bureau, Washington, D. C.

other situations, where artificial shade is found to be necessary, how properly to place shade where it will be most beneficial in reducing surface soil temperatures. Due to the complexity of the problem only horizontal soil surfaces will be considered.

Calculation of Solar and Sky Radiation Intensity for a Horizontal Surface

The best method for estimating horizontal surface radiation values[2] is the system outlined by the U. S. Weather Bureau (Fritz 1949). Fritz's equation is as follows:

$$Q_m = 1.94\left(\frac{r_o}{r}\right)^2 \cos Z\ (a''_m + 0.5 - 0.5a'_m) - D_m \qquad (1)$$

where the symbols are defined as follows:

Q_m = total radiation per minute on a horizontal surface from sun and cloudless sky, in gram calories per square centimeter (langleys).

r_o = mean distance between earth and sun.

r = actual distance between earth and sun.

z = zenith distance of the sun or angle of sun's rays with vertical (the angle of incidence in the Lambert cosine law).

a'_m = fraction of energy transmitted through the moist clean atmosphere considering depletion by scattering only.

a''_m = fraction of energy transmitted through the same atmosphere considering both scattering and absorption.

D_m = term including miscellaneous factors such as dust depletion and effect of ground reflection (albedo).

Subscript, "m", means that the symbol is to be taken at a particular "air mass," which is merely the path of light through the atmosphere referred to the vertical path as unity. The factor 1.94 in equation (1) is the solar constant in langleys per minute. For further expansion and application of this method the reader is referred to "Solar Radiation During Cloudless Days" (Fritz 1949).

[2]Letter of May 10, 1955 from Mr. T. H. MacDonald of the U. S. Weather Bureau, Washington, D. C.

Using Fritz's method the total cloudless solar and sky radiation values in langleys per minute were computed for the twenty-first day of each month for 39° north latitude and an elevation of 2760 feet, which is the elevation of the recorded surface soil temperatures. The above values are shown graphically in Figure 1.

In computing the radiation values in Figure 1, the correction, "D_m," for albedo and dust was omitted, due to the fact that Fritz (1949) showed only daily values and did not attempt to estimate the diurnal variation. Furthermore, since the corrections for daily values were small, one reviewer of this paper suggested that they be omitted.

Recording of Surface Soil Temperatures and Analysis of the Data

Now for the practical part of the experiment to record surface soil temperatures. One meter-square, 1×6 inch board frames were set in the ground and leveled. After filling these frames with sifted soil, the sensitive element of the Foxboro soil thermograph was pressed half-way into the soil (Aiken clay loam). Figure 2 shows the daily maximum temperatures from April 1954 to March 1955, inclusive. The important consideration in this study appears to be the extremes of surface soil temperature, and these occur when the surface soil is dry. Extremes may occur approximately eight days after an inch of moisture applied artifically during the summer months and after a slightly longer period of drying during the winter months.

Table 1, obtained from Figure 2 and the thermograph recordings for true solar noon, shows these extremes of surface soil temperature for select days of each month, following prolonged dryness. The computed noon values for solar and sky radiation from Figure 1 were divided into the true solar noon surface soil temperatures to arrive at a value of degrees F. of surface soil temperature per langley per minute.

In analyzing the values of degrees F. of surface soil temperature per langley per

TABLE 1. Tabulation of the true solar noon surface soil temperature recordings for cloudless days of extreme temperatures taken from Figure 2; the corresponding total solar and sky radiation values taken from Figure 1; and the empirical relationship between these two values, expressed in degrees F. of surface soil temperature per Langley per minute.

Date	True Solar Noon Surface Soil Temperature	Days Since Rain	Langleys Per Minute	Degrees F. Surface Soil Temperature Per Langley/Minute
Jan. 8, 1955	54	7	.86	62.8
Feb. 13, 1955	84	13	1.08	77.7
Mar. 7, 1955	110	10	1.27	86.6
Mar. 25, 1955	103	16	1.42	72.0
Apr. 22, 1954	140	?	1.59	88.1
May 18, 1954	142	9	1.65	86.1
June 2, 1954	147	23	1.665	88.3
June 20-22, 1954	159	12	1.676	94.9
July 13, 1954	156	....	1.65	94.5
July 28, 1954	162	....	1.62	100.0
Aug. 9, 1954	154	....	1.59	96.9
Aug. 22, 1954	147	....	1.55	94.8
Aug. 31, 1954	143	6	1.495	95.7
Sept. 9, 1954	144	....	1.435	100.3
Sept. 26, 1954	139	....	1.33	104.6
Oct. 15, 1954	136	....	1.17	116.2
Oct. 22, 1954	115	3	1.115	103.1
Oct. 29, 1954	112	9	1.065	105.2
Nov. 5, 1954	112	16	1.015	110.4
Nov. 24, 1954	87	9	.89	97.8
Dec. 20, 1954	74	10	.81	93.8

minute, it appears reasonable to assume that eventually a curve can be drawn showing the anticipated extreme surface soil temperatures for any day in the year, for a particular type of soil, elevation, latitude, etc. It is not meant to imply that these extreme temperatures will occur on the same day or even during the month of a particular year, but are temperatures which may be realized at a future date when there is sufficient dryness, cloudless sky, etc.

Figure 3 is presented to show the diurnal variation in radiation intensities and corresponding surface soil temperatures for selected extreme days in each month. The values were taken from Figure 1 and from the Foxboro thermograph recordings.

It should be noted that maximum solar and sky radiation always occurs at solar noon, whereas, maximum surface temperatures on level surfaces lag from one to two hours for all months except April and October, when the earth is at mean distance from the sun.

Effect of Artificial Shade on Surface Soil Temperatures, and Considerations for Properly Placing Shading Material

On August 4, 1953, a maximum recorded level surface soil temperature of 146° F. occurred at 1:30 p.m. for the unshaded sensitive element, whereas, on the same day, the temperature of the other element, shaded with shakes from the southeast and southwest so no direct radiation could reach it, reached a maximum temperature of 90° at 3:30 p.m. At noon the difference was 62°.

On July 29, 30 and 31, 1953, the sensitive element was placed 2½ inches north of a 7-inch wide shake. The surface temperature at 2:30 p.m. was 98° (maximum unshaded temperatures were 150° to 154°) at which time the shade became ineffective. At 3:30 p.m. the formerly shaded element had risen to 126-128°, an increase of 28° in one hour.

Thus, in view of the preceding examples, it can be seen that shade is very effective in reducing surface soil temperatures if it is placed properly.

By referring to a solar ephemeris it will be noted that the sun reaches its maximum northern declination on June 21 when it is approximately twenty-three and one half degrees. At this time the altitude, h, of the sun may be found by the following equation:

$$h = 90 - \text{latitude} \pm \text{sun's declination} \quad (2)$$

or, $90 - 39 + 23\frac{1}{2}$ equals $74\frac{1}{2}°$.

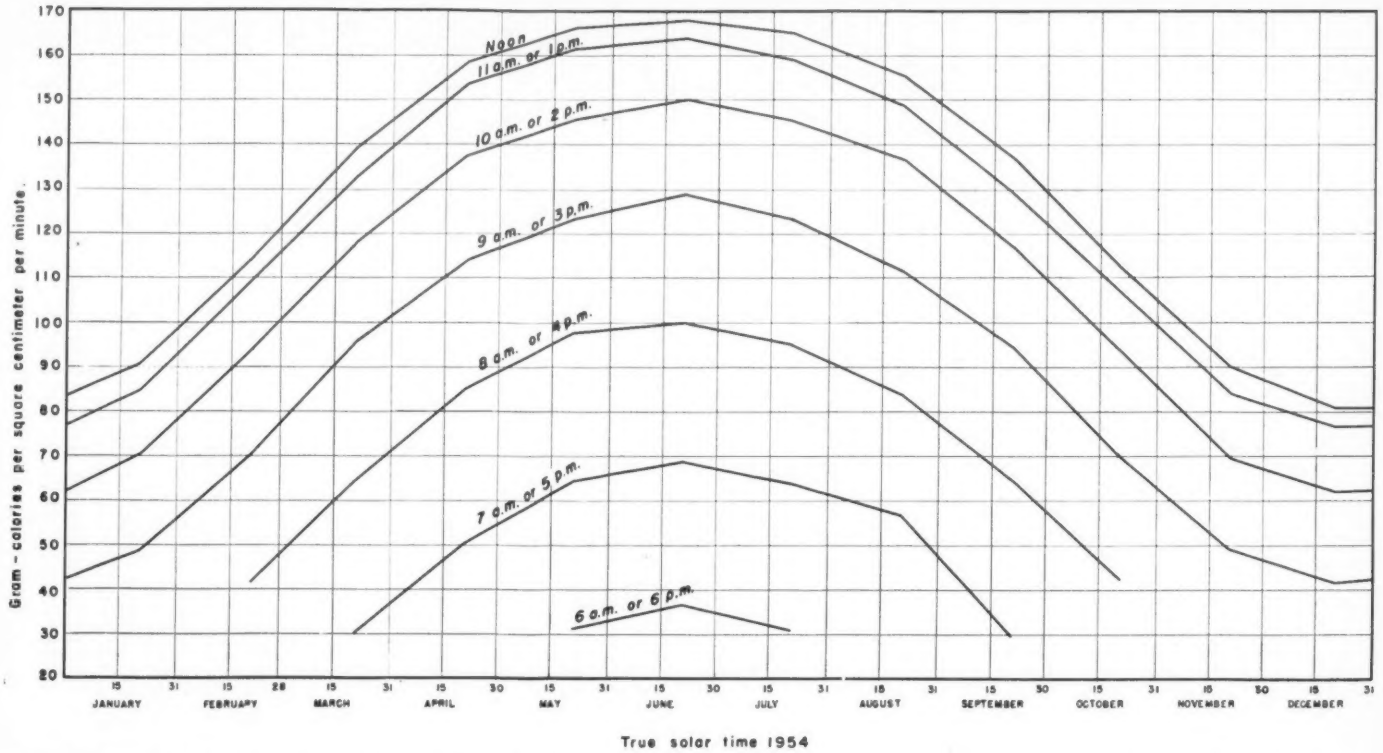

FIGURE 1. Total clear-sky solar and sky radiation values in gram-calories per square centimeter per minute, computed for the 21st day of each month for a level surface at 2760 feet elevation at north latitude 39°.

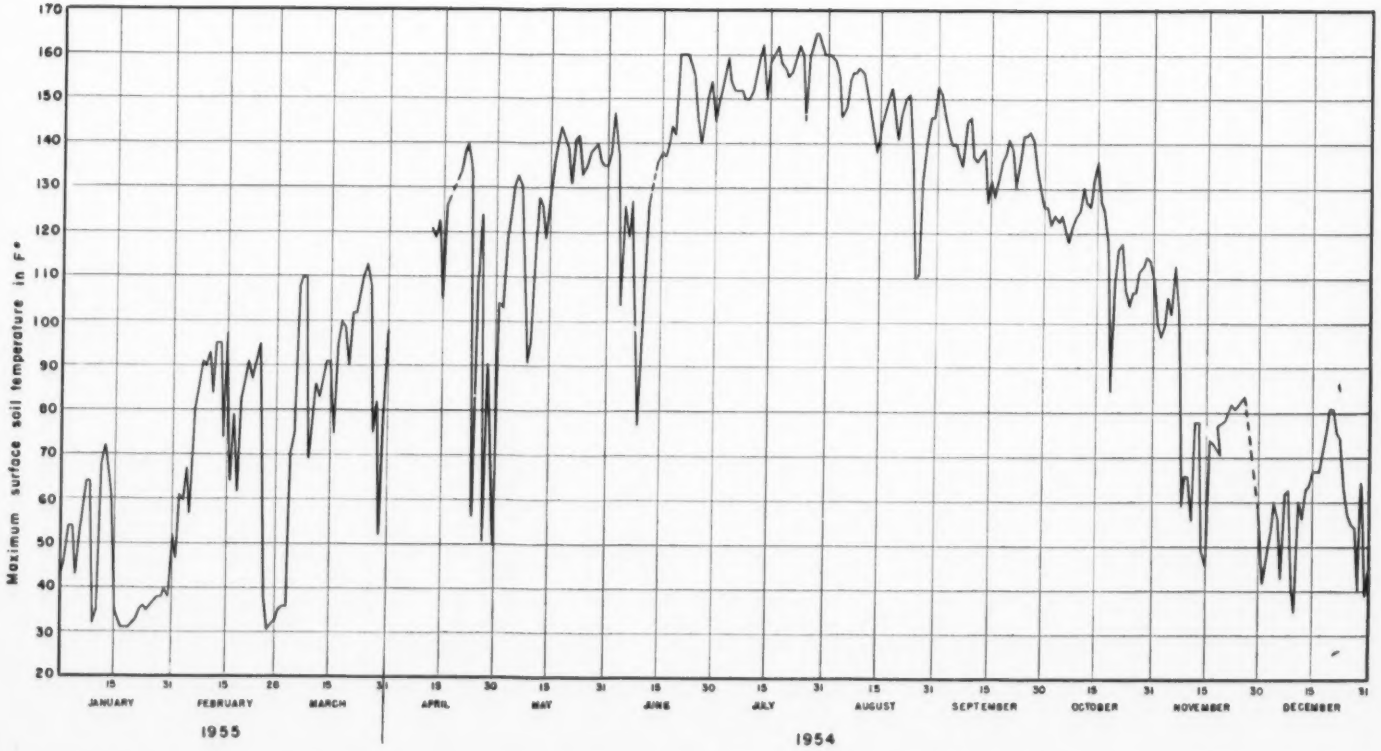

FIGURE 2. Daily maximum surface soil temperatures for a horizontal surface at an elevation of 2760 feet at 39° north latitude, as recorded by a Foxboro soil thermograph, from April 1954 to March 1955.

By using the tangent of 74½ ° it can be shown that for every inch that a seedling is north of a shingle-shade, the shade must extend 3.6 inches above the ground to produce its greatest cooling effectiveness.

Again, by referring to "Tables of computed altitude and azimuth for latitudes 30-39 degrees" published by the U. S. Navy Department Hydrographic Office, it will be noted that the sun passes through an arc of the sky equal to 160 degrees during the hot surface soil temperature hours of 10:00 a.m. to 4:00 p.m. (See Figure 3), on June 21. This means that on level and due north and south slopes, the shade should be placed 24° west of south to be most effective.

By using the tangent of one-half this angle and then multiplying by two we ascertain that flat shade should be 11-1/3 inches wide for every inch that the seedling is northerly from it. Obviously, this type of shade is impractical. A pointed, V-shaped or semi-circular plastic shade which could be pressed into the soil close to the seedling so as to shade from the southwest and southeast, would be a desirable type of shade from a practical and economical viewpoint.

Effect of Irrigation and Rain on Surface Soil Temperature, with Special Consideration as to Amount of Reduction and Duration of Effect

On May 17, 1954, at 1:00 p.m. a level surface plot of bare mineral soil was sprinkled with the equivalent of one-inch of rain.

On May 18, 19 and 20 the watered plot was 41, 26 and 17 degrees lower than the dry soil plot and on May 24 it was only six degrees lower.

By referring to Figure 2 it can be seen that rain will lower the surface soil temperature by as much as 50 degrees and that 5 to 16 days later, depending upon the amount of precipitation in the storm, extreme surface soil temperatures will occur due to the drying out of the surface.

Effect of ⅞ Inch of Sawdust Mulch on Surface Soil Temperatures

In an experiment with sawdust, the sensitive element of the thermograph was pressed half way into the surface of the sawdust and was not in contact with the mineral soil.

At 8:00 a.m. on May 31, 1954, one of the plots was covered with a ⅞-inch layer of dry sawdust and sprinkled with a one-inch layer of water. The maximum surface soil temperatures of the sawdust plot were within one to two degres of the dry soil plot for the succeeding four days. Apparently the thin surface layer dried out very rapidly and obviously did not show the same cooling effect of water on a bare mineral surface.

Again at 4:00 p.m. on September 27, 1954, sawdust was soaked in water for four hours and a ⅞-inch layer spread over one of the plots. The following day the maximum surface temperature of the sawdust plot was fourteen degrees lower than the dry soil plot, but thereafter, for the succeeding six days, was only two to four degrees lower.

Finally, on November 10, 1954, the sensitive element was placed in the sawdust plot. On November 11, a rain soaked both the bare soil and the sawdust plots. The maximum surface temperature of the sawdust plot was warmer for the succeeding two days by two degrees; on the third day it was nine degrees warmer than the bare soil plot. On November 13 and 14 the plots were again soaked by rain, and for the succeeding five days the sawdust plot was warmer by from two to eight degrees. The subsequent five rainless days showed the sawdust plot to be from fourteen to seventeen degrees warmer than the bare soil plot.

The data in the foregoing tests indicate that during the wet months following rain the maximum surface soil temperature of the sawdust plot was as much as 17° warmer than the bare soil. It would seem that the temperatures of the sawdust plot

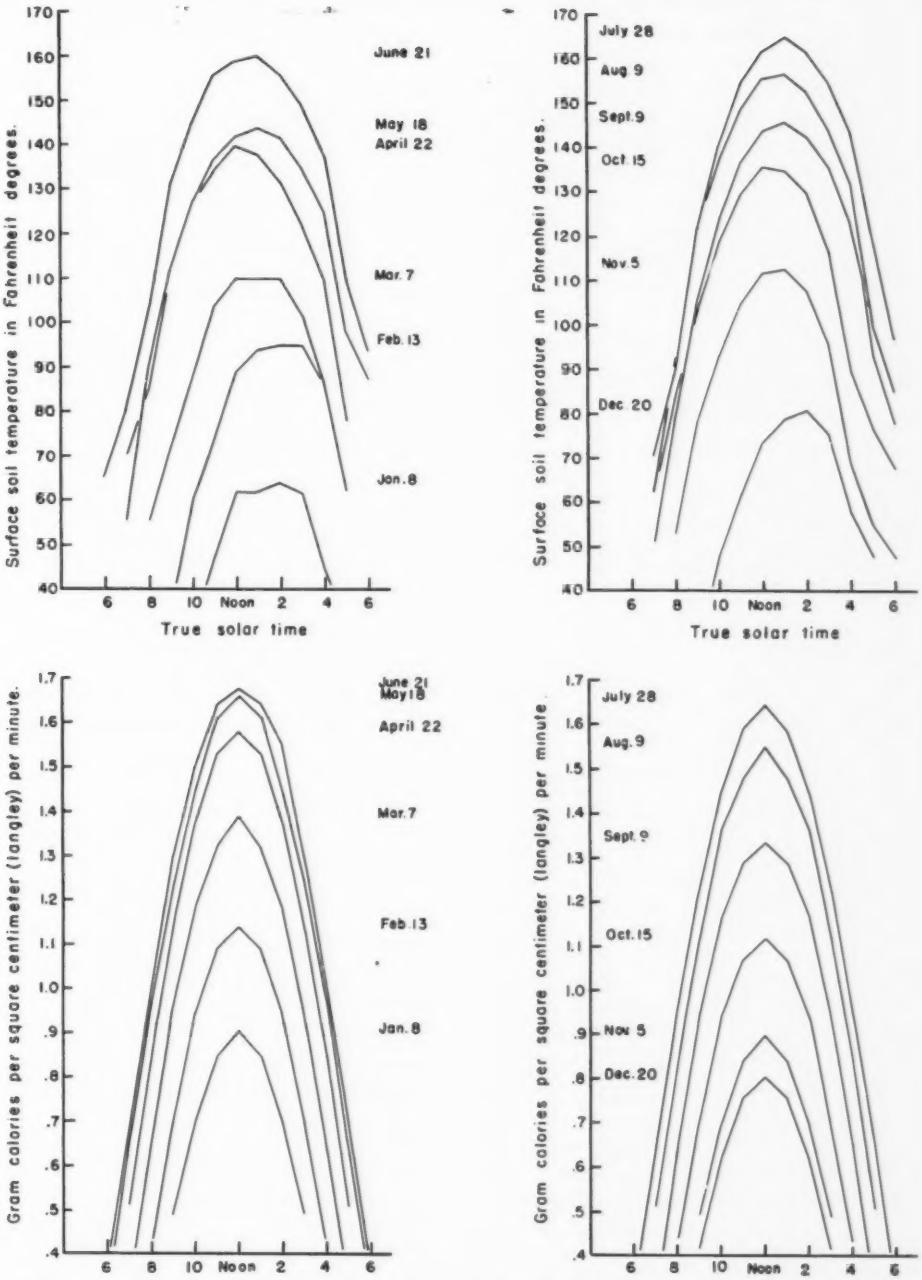

FIGURE 3. Upper portion of figure shows diurnal surface soil temperatures for selected extreme days from April 1954 to March 1955. Lower portion shows corresponding diurnal radiation intensities.

would be similar to the duff and litter of the forest floor. (Vaartaja, 1954) has shown that the presence of humus and fine litter favored extreme diurnal variations in temperature. It is possible that these extremes of temperature in duff and litter, during the months of April and May when radiation intensities are high (see Figure 1) and seedlings are germinating, may be the primary cause of the failure of seedlings to establish themselves in duff and litter. It is a well-known fact that Ponderosa pine seedlings will become established on bare mineral soil when they fail in similar locations which are covered with duff and litter.

Furthermore, the results of these experiments with sawdust, under California conditions, would suggest that the mulching of unshaded planted seedlings is more of a detriment than a help as far as survival of seedlings is concerned.

Practical Results of Shading in Field Plantings

On April 17 and 24, 1953, 300 ponderosa pine seedlings (2-0) were planted on moderate south to southwest slopes at an elevation of 3000 feet. Approximately half of the seedlings were shaded with 7×18× 1/12 inch reject rotary box shook. The planting was examined for survival on May 12, 1954. Eighty percent of the shaded seedlings had survived and displayed two to four inches of new vigorous growth. At this examination forty-seven percent of the shade was broken or ineffective due mostly to trampling by cattle. In contrast, 20 percent of the unshaded seedlings survived and many of these appeared to have low vigor, even to the extent that terminal buds had not opened yet.

On this same planting some unshaded seedlings, in addition to those above, had their bases protected with cotton batten or 1½ inch galvanized metal pieces. An accurate record of the stem-base protected seedlings was not kept, but it appeared as if the seedling survival of the cotton-protected bases was 82 percent and that of the metal-protected bases 69 percent. This would indicate that the greater survival of the shaded seedlings is attributable to the milder surface soil temperatures alone, and not to the influence of a decreased transpiration rate caused by the shading of the needles.

Summary

This report emphasizes the importance of surface soil temperatures to seedling survival. Cloudless sky horizontal surface solar and sky radiation values for sunlight hours throughout the year were computed for the location of the Institute of Forest Genetics near Placerville, California. Year-long daily recordings of maximum surface soil temperatures by a Foxboro soil thermograph are graphically shown and correlated with solar and sky radiation values for selected days of extreme surface soil temperature. It appears that extreme surface soil temperature possibilities can be anticipated eventually from computed radiation curves.

Important considerations for properly placing artificial shade for level and north and south exposures, the quantitative effect of shade in reducing soil temperatures, and the quantitative and durational effect of rain on soil temperatures are described. The effect of extreme surface temperatures of duff and litter during the seedling germinating months is suggested as a possible reason for seedlings failing to establish themselves. Finally the results are given of an experimental planting to show the effect of shade and the subsequent 400 percent increase in survival.

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Forestry and Related Research in North America.

Prepared by Frank H. Kaufert and William H. Cummings. 1955. Society of American Foresters, Washington, D. C. 280 pp. $5.00.

REVIEW by Edward N. Munns

Concord, California

Forest research has passed another milestone. This time, it is the 25th anniversary of the Federal McSweeney-McNary Forest Research Act. In this legislation was spelled out for the first time an organizational and financial program in forestry research. With it as a stimulus and with forestry increasing in importance, research took its place as a recognized forestry activity.

Sharply aware of the growing importance of research, the Society of American Foresters initiated a reappraisal of the situation in forestry research throughout North America. With financial and moral support from others, it launched its "reexamination of the whole structure of forestry research programs." Two competent foresters made the study under the over-all direction of a steering committee.

The study had a 3-pronged purpose: to determine whether progress was satisfactory, what was the present status, and what were the future goals. The conclusions reached were that progress in forest research has been great, the present effort inadequate, and the need enormous. The over-all highlight is that in the United States a 4.4-fold expansion in forestry research expenditures is required by 1978. Comparable data for the neighboring countries are not given.

The study provides little comfort to those foresters who argue for a moratorium on research until practice catches up with knowledge. Instead it calls for a great expansion in all lines of work, and immediate and rapid expansion in a few. The financial increase of 440 percent in 25 years does not appear materially significant in view of the 1000 percent increase in the past 25. Neither does it appear out of line with present national economic conditions or the growing intensification of forestry practices. When these percentages are translated into dollars, the overall figure of $200,000,000 does seem a bit startling. If the total is discounted for the tremendous amount of industrial research by wood-using industries, one can take the proposed $75,000,000 for truly forestry research in stride. Certainly in view of our great wild land area we should not be niggardly in efforts to develop a real know-how and understanding if we are to meet the ever increasing pressures upon its resources.

The study stresses the great contribution the forest schools can make. Suggested is the idea that the forest schools increase their participation in research ten-fold in the next 25 years. This would mean stepping up their present expenditures of $1,676,000 to $15,000,000. At present the schools' effort amounts to 3.7 percent of the total of all research, but the proposed increase would have them doing 7.5 percent of the job. This expansion would take place with the declining emphasis on research in industry and in the Federal Government. In the light of experience, this would seem somewhat unrealistic and evidence of some wishful thinking.

Much encouragement could be given to re-

search workers to advance their formal training if research agencies would take some positive steps in that direction. One way would be through greater use of men with doctorates in such fields as physiology, soils or ecology rather than to depend so heavily upon forestry graduates. Granted that undergraduate work in forestry provides the best background for forestry careers, it is not essential to a successful career in forestry research. This proposal should not upset the forestry schools today as it did a decade or so ago when graduates were having some difficulty in finding jobs. That the earlier use of such trained men did not work out particularly well in practice was due more to lack of skill in their utilization than to lack of forestry background. Today the need for work in the basic sciences is so well understood that many subject matter specialists could be employed and fitted into a going research program.

Salaries of research men are a part but only a part of the personnel problem. They constitute a major part when organizations compete for an individual worker. All too often, this individual is not adequately recognized in his own unit until employment elsewhere is under consideration. Then there is scurrying around to find ways of meeting the offer. In many agencies of government, the difficulties in advancing or recognizing a researcher on the basis of his contributions alone are well nigh insurmountable. It therefore becomes necessary to assign the man more and more administrative duties if he is to be advanced. To the extent that these routine or other duties cut into his research time—and they often do to a marked degree—they reduce the quantity of research done if not the quality as well. Few research administrators seek ways of keeping the individual worker from becoming bogged down in paper work; instead they generally take the easiest course and let research suffer.

The feeling, and in part the practice in some Federal agencies, that every research man should have from one to several years' training in administrative jobs before entering upon research may be on its way out. However, lack of such experience as a ranger prevents many men in the Forest Service from transferring out of research into administrative jobs of similar standing, even when all concerned recognize the desirability from the research standpoint. These and similar situations confronting personnel should be topics for discussion in the proposed forestry research conference as recommended in the report.

The money estimates for future research, while large in total, can be accepted. Anyone who has developed estimates for research covering even such a short period as five years can appreciate the inherent difficulties in making estimates for 25 years appear realistic. Great credit attaches to the study for providing overall estimates which in the light of present day conditions seem reasonable if unobtainable.

Much greater confidence in the estimates would have resulted had there been some discussion of the processes used to derive a figure for just one activity as an example. Fewer questions might then have arisen. As it is, there is too much variation between estimates for some of the activities. Thus the maximum increases recommended for forest soils is 15×, genetics 12.5×, watershed 11.6×, and recreation 10×. The smallest increases are for range and economics, both 2.5×. One can appreciate how enthusiasm for an activity, especially a new one with energetic supporters, will color one estimate whereas lack of understanding of another field will tone down its place in the sun.

It may be completely academic to question individual recommendations in view of probable changes in over-all economic conditions. It is felt that the study was a little soft on genetics, severe on range, and unrealistic on fire research. We do not discount the advances possible through genetical research but when much greater expenditures are suggested for genetics than for soils, physiology, or fire, then we fear that someone was carried away by sales talk or enthusiasm.

Unfamiliarity with western watershed problems and the condition of the range on them is probably at the root of the relatively small increase suggested for range work. The immense areas of nearly exhausted forest, brush and grass lands used as range by livestock and big game and punished by decades of overuse under unfriendly skies, call for wider appreciation of problems to say nothing of more research. All too often, thinking on these lands by the uninformed, relegates their problems to a minor category. When it is realized that land has been destroyed, site quality lowered, native forage rendered almost extinct, and needed water resources lost or damaged, then one feels the estimates are not in keeping with

need. A great upsurge in range research of all kinds is required to develop new and more nutritious forage, to rehabilitate ruined soils, and turn worthless cactus and brush areas into a productive resource.

At this point too one is annoyed by the advice given for only in this section are spelled out in detail not only the kind of research envisaged but also instructions as to its organization. How greatly the study misses the mark here is also shown by the lack of appreciation of need for economic research as the suggestion is made that any such need can be met by some one acting in an advisory capacity. If it were intended that the forest economists would also handle range problems, that is not mentioned. The tremendous scope of the range problems, their social and economic significance, and their vital import to states, communities, the Indians, and the nation suggest the need for far more recognition by foresters of their stake and interest in range.

The discussion of economics could well have been sharpened had a separation been made between the research and the collection of data on timber resources by surveys. The physical task of making the resource inventory is so enormous and costly and requires so much in personnel it overshadows the basic economic research and research needs. This is borne out by the fact that about $1,250,000 of the $2,000,000 now spent is for survey, leaving only $750,000 as the amount spent for all other economic research. This would be merely doubled in 1978, whereas a million more is needed for range economics alone.

The fire research section should be read by all foresters no matter what their job. This is not so much for what the study reports as for what it does not specifically say or bring out. The recommendations are for a 7-fold increase, or for $3,000,000 to replace the present $420,000, with a 3-fold increase in ten years. Such an increase is desirable and long over-due. Whether the sums are sufficient is doubtful so long as the profession continues to be complacent over fire. The continued reliance of land managers on brawn and machines instead of on brains and technical knowledge of complicated physical and chemical phenomenan, is resulting in our continuing and staggering losses of resources and accompanying expenditures for fire control.

The report brings out publicly for the first time, not in words to be sure, the most shameful blot on all forest research development. It shows the delinquency of fire control agencies, especially the States, in their attitudes toward fire research. For years, this has been kept under wraps but the data in the report show the real situation. Since the adoption of the Clarke-McNary Act 30 years ago, the Congress has provided large and growing sums to the States for fire control purposes. These have been matched in greater or less degree by the States themselves. Despite the large amounts so made available none of this money has been channeled into research, or if so, on such a small scale as to be unnoticed. Yet, State forestry agencies owe their existence in large measure to the continuation of the fire problem. So long as such a niggardly attitude attaches to these public agencies, so long as they fail to support efforts to obtain funds for fire research, they continue to demonstrate their lack of faith in research.

Not all the blame attaches to State agencies. The allocation of only $250,000 out of the present total of $7,000,000 for all Federal "Forest Management" research shows that the red-headed stepchild attitude toward fire research prevails in the Federal agencies as well.

For some reason the study ducks a discussion of personnel problems in fire research, but it is believed that herein lies another major trouble. So far most fire research personnel have been drawn from the ranks of fire fighters, many if not most of whom have no basic understanding of or training in the laws of combustion. Where technical skills have been employed, there is a real question as to whether their skills have been fully utilized, though one such man made some outstanding contributions. While the financial picture could be changed overnight by the action of administrative foresters alone, the problem of getting high-grade trained personnel cannot be solved satisfactorily under 5 years. In this situation, all foresters ought to be concerned.

The inclusion of recreation research is a source of real joy. All the factors involved in our standard of living are developing pressures upon our wooded areas, of which recreation is perhaps the least appreciated. Within a very few years the demands for desirable recreational areas will begin to affect the management and uses of land, both public and private. The recommendation for a ten-fold increase in recreation research is not too much, especially if the work is materially enlarged in the next

few years. Unless it is undertaken with vigor, daring and imagination, managing foresters will find themselves saddled with an incubus for whose removal there will be no solution.

Recreation research is another field in which the State agencies can and should play a major role. They should finance or greatly assist in financing recreational research in whatever agency appears to offer the best facilities or opportunity. In addition, the Federal research agencies, now deeply engrossed in well established activities, should give serious thought to the early expansion and development of this activity. The fact that intensively used recreation areas are in another competitive administrative agency ought not be used as an excuse for not launching a research program of real magnitude into this field. So far the major recreational problems are not being given the same degree of intensive study that the situation merits, and most research groups show little concern with the problem.

There appears to be a continuing effort to keep all forest products and utilization research within the forest research tent. Naturally the study had no choice but to include a discussion of products research as the Forest Research Act of 1928 included it. The time is approaching when many of the activities included in the generic term of "forest products" will be considered as an associated part of forestry rather than an integral phase. Certainly few "dirt foresters" are much interested or concerned with the specialized details of paint or varnish manufacture, glues, or paper making. Basically, forestry should be kept to those things which are directly associated with the land even as in agriculture.

The discussion of products in the study will please but few specialists, or for that matter, even the dirt forester. It fails to provide an adequate picture or understanding of the various activities it embraces. There is no real breakdown of the huge sums involved, either present or future. Consequently the reader must piece the fragments together to get some appreciation of the estimates. Undoubtedly those in the highly competitive industries are not too anxious to have much public discussion of their research activities or problems. The net result is an inadequate treatment of the subject. Sometime, someone will be able to give us a true picture of that work in the utilization field in which foresters as such are directly interested.

Missing from the study is a sympathetic consideration of dendrology which here is included as part of physiology rather than of genetics. However, even this discussion omits any comment on arboreta research. With a large National Arboretum near the nation's capitol and the various other well-known arboreta scattered around the country, the omission stands out sharply.

The reports on research in Canada and Mexico are not as detailed or as complete as those for the United States. This is understandable though in Canada the problems and methods of solution approach closely to our own. The Canadian report compiled by S. T. Dana follows the general treatment of research here but does not discuss the organic troubles which we face so immediately. It is presumed that finance, personnel, and organizational difficulties are much the same in Canada as here.

The forestry research in Mexico is described by Dr. Enrique, Director of the Mexican Institute of National Resources. The discussion reflects all too well the stagnant situation which is common to many another nation of similar conditions. Apparently there has been much exploratory work but little technical research on many basic forest land managing problems. Were it not for the language barrier, American foresters might be able to help the Mexicans in their struggle to accomplish something in research. One cannot read this section without feeling a desire to do something specific to help overcome the handicaps which the Mexican foresters face.

All in all, "Forestry Research" is one of those books that every forester should read if not own. Few foresters know enough about what is going on in forestry research to be able to understand the problems which foresters generally face or those which forestry research faces. Certainly no one interested in the future development of a large segment of forestry can afford not to be acquainted with it. Regardless of how organizations, institutions, or individuals may react to the recommendations in whole or part, these should be discussed thoroughly. How far they are adopted and become a reality will depend largely upon the extent to which all those interested in forestry progress will agree that more and better forestry research is needed.

Wind Profiles in a Small Isolated Forest Stand

BY
WILLIAM E. REIFSNYDER

How the wind blows in forest stands and in their boundary regions concerns the forest manager in a number of important ways. Since structure of the timber stand affects the behavior of wind in and around it, the distribution of seed needed for natural regeneration following cutting will be influenced by the pattern and intensity of cut. Further, the likelihood of damage from blowdown of trees left can be influenced greatly by the cutting practice used. Forest fires usually behave in direct response to local winds. Knowing how winds behave in and around forest stands can thus help fire fighters pick the strategy best suited to each fire station.

Several workers have studied the behavior of wind well inside a forest stand (Fons, 1940; Gisborne, 1941; Kepner *et al*, 1942; Latimer, 1950), but few have studied the variation of the wind at the edge (Iizuka, 1952). Unanswered questions include: How far from the edge of a stand does the wind reach conditions similar to those prevailing far inside? How does the wind profile change through the entrance region? How does this transition change with different conditions of air stability? In selecting or constructing models for the derivation of relationships having practical applications, how large must models be to cover the total range of boundary conditions?

A partial answer to these questions was made possible when a small isolated stand of ponderosa pine trees was artificially created on a desert playa. Although the stand was created for another purpose, instruments were installed to obtain suitable wind measurements.

Description of Stand

On a dry lake bed, 145 open-crowned ponderosa pines characteristic of Southwestern trees were placed 20 feet apart in staggered rows, also 20 feet apart (Figs. 1 and 2). This arrangement produced a stand measuring 160 by 320 feet, or about 1.2 acres. The stand area and immediate vicinity were levelled and stabilized with soil cement.

In the prepared stand, trees varied in height from 36 feet to 64 feet, averaging 51 feet. Average height to base of crown was 16 feet. Diameter at breast height ranged from 8 inches to 16 inches and averaged 13 inches. The stand was well stocked by number of trees per acre, according to Lexen (1939). The stand-density index calculated according to Reineke (1933) was 0.20. Crown area, expressed

When this study was made, Reifsnyder was Meteorologist at the California Forest and Range Experiment Station, which is maintained by the Forest Service, U. S. Department of Agriculture, at Berkeley, Calif., in cooperation with the University of California. He is now Assistant Professor of Forest Meteorology, Yale University. John A. Hartford Foundation Program in Forest Biology.

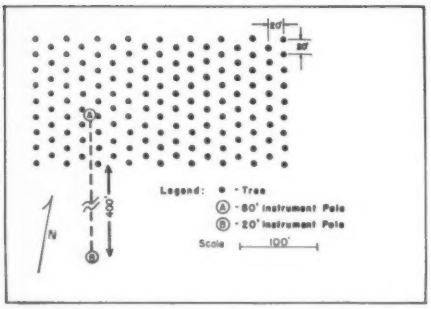

FIGURE 1. Plan of tree stand showing location of instrument poles.

at the ratio of vertical projection of tree crowns to total area occupied by the stand, was 20 percent. This expression is of interest in wind profile studies and will be the measure of stocking used to describe this stand in the remainder of this report.

Instrumentation

Four rows in from the west end of the stand, and nearly equidistant from the sides, an 80-foot wooden pole was erected. On this were mounted Robinson-type 3-cup anemometers at the following levels: 5, 16, 33, 51, 66, and 80 feet. In addition, an 8-contact direction vane was located at the 80-foot level. In order to obtain a reference velcocity, another 3-cup anemometer was located at the 20-foot level 400 feet south of the stand.

Records of every 1/10-mile of wind were obtained by removing 5 of the 6 contacts in the 1/60-mile contacting mechanism of the anemometers. An Esterline-Angus operation recorder was used to obtain simultaneous records from the seven anemometers and the direction vane.

Anemometers were calibrated before installation in a 3-feet by 3-feet, low-speed wind tunnel.

Reduction of Data

A 6-minute period was selected for obtaining mean wind speed. Six minutes was the shortest interval in which anemometer records could be read accurately. A longer period was not used because of the danger of masking fluctuations in the mean values of direction and speed. The 6-minute interval also had the advantage of making chart reading relatively easy because the number of contacts in 6 minutes directly

FIGURE 2. End view of stand looking west.

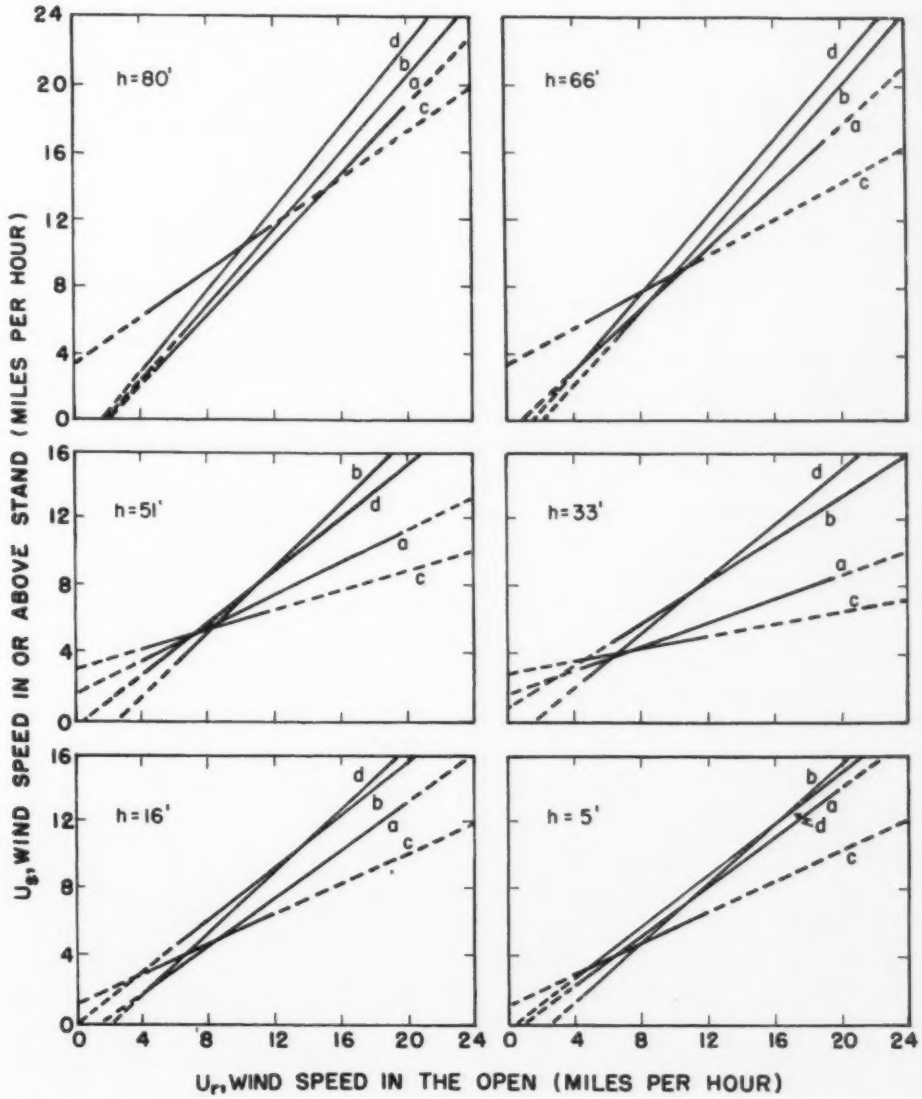

FIGURE 3. Wind speed at various heights as a function of wind speed at 20 feet in the open: a) Lapse conditions, 250 feet travel; b) Lapse, 70 feet travel; c) Inversion conditions, 250 feet travel; d) Inversion, 70 feet travel. Solid part of lines indicates range of data.

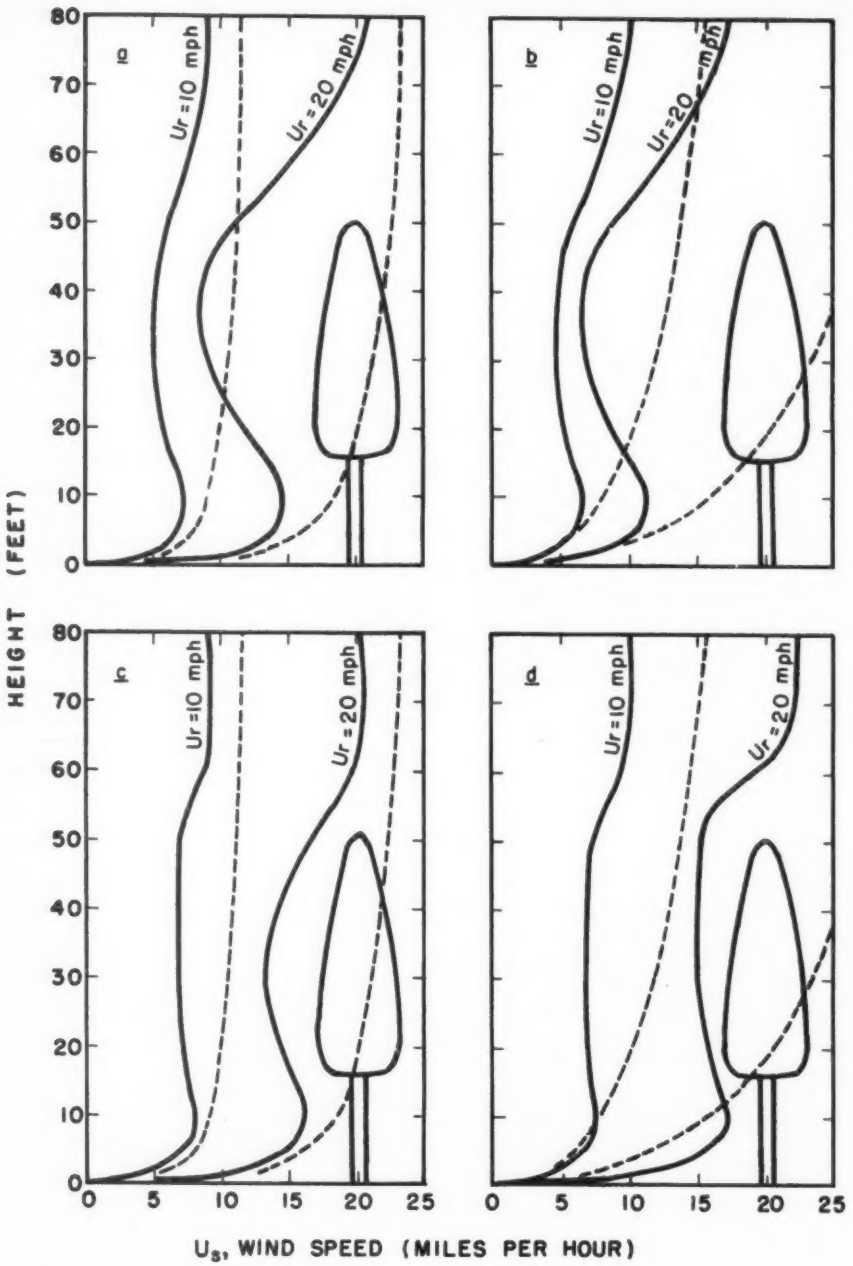

FIGURE 4. Wind profiles in forest stand: a) Lapse conditions, 250 feet travel; b) Inversion conditions, 250 feet travel; c) Lapse, 70 feet travel; d) Inversion, 70 feet travel. Broken lines are comparable profiles over bare ground; U_r, wind speed at 20 feet above ground in the open.

TABLE 1. Summary of constants a and b in regression equation $U_s = a + b\ U_r$[1]

Level of wind speed, U_s (*feet*)	Lapse conditions				Inversion conditions			
	250-ft. travel		70-ft. travel		250-ft. travel		70-ft. travel	
	a	*b*	*a*	*b*	*a*	*b*	*a*	*b*
80	—2.22	1.15	—2.10	1.12	3.32	0.69	—2.05	1.21
66	— .63	.92	—2.02	1.11	3.35	.55	—1.64	1.16
51	1.64	.49	—2.64	.96	2.93	.30	—0.49	.79
33	1.44	.36	.71	.63	2.75	.19	—1.36	.81
16	— .54	.68	— .12	.77	1.28	.43	—2.09	.92
5	— .34	.72	— .67	.77	0.99	.46	—2.33	.88

[1] U_s = wind speed in tree stand, m.p.h.; U_r = wind speed at 20 feet in open, m.p.h.

indicated the wind speed (uncorrected) in miles per hour.

Continuous records were taken for 4 typical clear desert days, resulting in 992 6-minute observations. All observations in which the wind direction was parallel to the long axis of the stand were selected for analysis. This yielded two groups, one in which the wind travelled through 70 feet of stand before reaching the anemometer pole; the other, through 250 feet.

These groups were then subdivided into three broad temperature gradient classes: Inversion (sunset to sunrise), lapse (2 hours after sunrise to 2 hours before sunset), and neutral (all other observations). The number of observations in each class was:

Temperature gradient class	*Wind travel 250 feet*	*Wind travel 70 feet*
Inversion	21	90
Lapse	27	48
Neutral	16	2

Because of the small number of observations in the "neutral" class, the analysis was limited to lapse and inversion conditions.

Wind Profiles

For each of the four classes analyzed, scatter diagrams of wind speed in the stand (U_s) against wind speed at the 20-foot anemometer in the open (U_r) were prepared for each of the six levels in and above the trees. Since data appeared to fall in a straight line, regression lines were fitted (Fig. 3). From these, wind speed-height curves were prepared (Fig. 4). Constants a and b for the equation of the form $U_s = a + bU_r$ of each regression line in Figure 3 are given in Table 1. Correlation coefficients for each regression line and the corresponding correlation coefficient at 1 percent level of significance are given in Table 2.

Effect of Distance from Edge of Stand on Wind Profiles

An analysis was made to assess the variation in reduction of wind by the tree crowns with difference in distance from stand edge. This was accomplished by computing the ratio, U_s over U_r, using wind speeds at the 33-feet level in the stand (at the center of the tree crowns) and at the same level in the open. The wind in the open was obtained by adjusting 20-foot reference wind speeds to the higher level.[1] The reduction in wind speed was plotted against distance from edge of stand, and although more points would be neces-

[1] This adjustment was made on the basis of curves given by C. W. Thornthwaite (1949). These curves give ratios of wind speeds at various heights over smooth level ground for inversion and lapse conditions.

TABLE 2. Correlation coefficients for regression lines in Figure 3.

Level of wind speed, U_z (*feet*)	Lapse conditions		Inversion conditions	
	250-ft. travel	70-ft. travel	250-ft. travel	70-ft travel
80	0.972	0.982	0.668	0.976
66	.945	.984	.686	.977
51	.920	.948	.662	.945
33	.903	.895	.376	.969
16	.940	.951	.800	.971
5	.926	.974	.804	.976
Significance at 1% level	.487	.368	.549	.270

sary to determine the curve accurately, trend lines were drawn (Fig. 5). Reduction in wind speed probably reaches zero about one tree height to windward.

Discussion

All correlations except the one for inversion conditions and 250-foot travel at the 33-foot anemometer were significant at the 1 percent level. In addition it should be noted that all correlations for 250-foot travel and inversion conditions were lower than any other. Considering the narrow spread of data (4 to 12 miles per hour) conclusions involving this inversion class, especially at wind speeds above 12 miles per hour, should be accepted with caution.

Comparison of Lapse and Inversion Conditions. Inspection of Figure 4 reveals that lapse and inversion profiles in the isolated stand had essentially the same form. Certain marked differences may be noted:

1. For a given 20-foot reference wind speed, winds in the trunk region of the stand during inversion conditions at night were approximately two-thirds the speed of daytime winds.

2. Although the reduction of wind in the tree-crown region is about the same under lapse or inversion conditions for light (10 m.p.h.) winds, the reduction is greater under inversion conditions for moderate (20 m.p.h.) winds.

"Edge" Effects. In the interior of an "infinite" stand—that is, one extending large distances parallel and perpendicular to the direction of the wind—no net vertical wind velocities can occur. In a semi-infinite stand, one which extends a large distance perpendicular to the wind but has a finite forward edge, vertical velocities arise in front of and in the entrance region. Iizuka (1952) has shown that vertical velocities arise in the entrance region of windbreaks. A finite stand, or one which has a forward edge and small horizontal extent perpendicular to the wind, will also produce horizontal components perpendicular to the major axis of air flow. No information is available on the magnitude of these effects. Accordingly, data on edge effects obtained in the present study must be interpreted in a qualitative sense.

1. In low-density stands similar to the one studied (20 percent stocked) in lapse conditions, the infinite wind profile does not fully develop within 70 feet or four rows of trees from the stand edge. It is likely, however, that wind conditions of an infinite stand are reached 250 feet or 13 rows of trees in from the edge.

2. In lapse conditions, moderate winds suffer a greater percentage reduction than light winds, but they both reach maximum reduction at about the same distance from the edge.

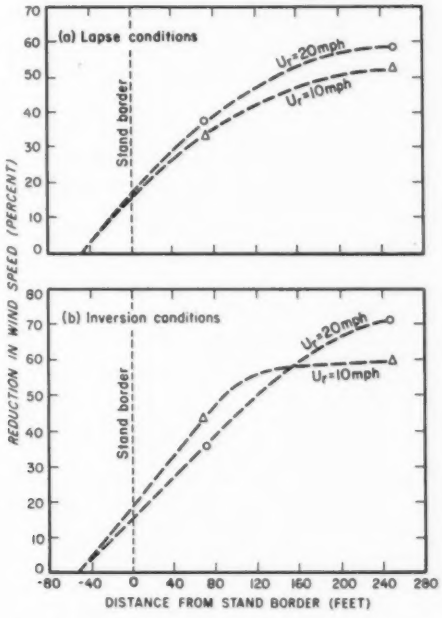

FIGURE 5. Reduction of wind speed by ponderosa pine stand—33-foot level.

3. In inversion conditions, on the other hand, light winds reach maximum attenuation closer to the stand edge than do moderate winds. In the stand studied, it is probable that 10-m.p.h. winds were reduced the maximum amount 100 to 150 feet in from the edge, whereas 20-m.p.h. winds may not have reached this point 250 feet in.

Comparison with Other Data. Because of differences between this stand and those studied elsewhere and in methods and techniques of measurement, quantitative comparisons with previous work are not possible. However, certain useful qualitative comparisons can be made.

Wind profiles under lapse conditions can be compared in four forest stands (Fig. 6). Data are given by Gisborne (1941) for a dense stand of conifers with understory in northern Idaho; wind speeds are for mid-afternoon on a typical summer day. Latimer (1950) reports winds under daytime conditions in a hardwood jungle. Fons (1940) measured winds in an even-aged ponderosa pine stand in California which

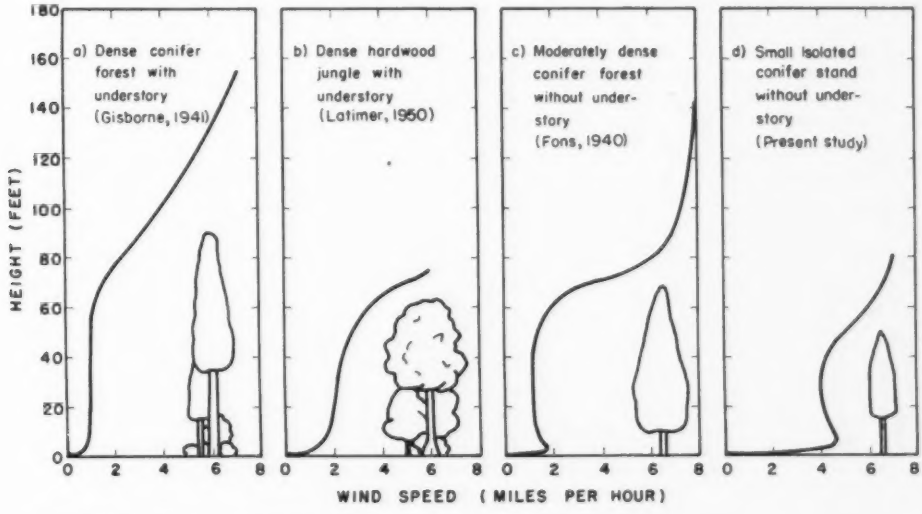
a) Dense conifer forest with understory (Gisborne, 1941)
b) Dense hardwood jungle with understory (Latimer, 1950)
c) Moderately dense conifer forest without understory (Fons, 1940)
d) Small isolated conifer stand without understory (Present study)
HEIGHT (FEET)
WIND SPEED (MILES PER HOUR)

FIGURE 6. Comparative wind profiles under lapse conditions.

had a computed stocking of 62 percent based on number of stems per acre.

The following points may be noted from visual comparison of the four lapse profiles.

1. Wind speed is nearly constant in the tree crown region, although a small increase with height occurs in stands with understory (Figs. 6*a* and 6*b*), and a definite minimum occurs in the crown region of stands without understory.

2. Wind speed in the tree crown region is decreased much more by the moderately stocked stand (Fig. 6*c*.) than by the sparsely stocked stand (Fig. 6*d*).

3. A relative maximum of wind speed occurs in the trunk region of stands without understory. This maximum occurs at approximately the halfway point in the trunk space. In stands with dense understory, wind speed is essentially constant from near the tree tops to within a few feet of the ground where a sharp wind gradient occurs.

Inversion profiles also show marked similarities (Fig. 7). Two points may be noted.

1. In all inversion profiles, wind speed in the crown region is more nearly constant with height than it is in the lapse profiles.

2. A secondary maximum occurs in the trunk region in the two stands without understory. However, this maximum is not as sharply defined as in the lapse profiles.

Conclusions

1. Wind profiles from an isolated, 145-tree stand of ponderosa pines show qualitative similarity to profiles obtained in similar stands of greater areal extent and greater density.

2. "Infinite-stand" wind profile was not fully developed 70 feet in from the stand border. The data tentatively suggest that a fully developed "infinite-stand" profile did occur 250 feet in under lapse conditions.

3. Under inversion conditions, the wind profile reached its full development nearer the edge for light winds (10 m.p.h.) and farther from the edge for moderate winds (20 m.p.h.), as compared with lapse con-

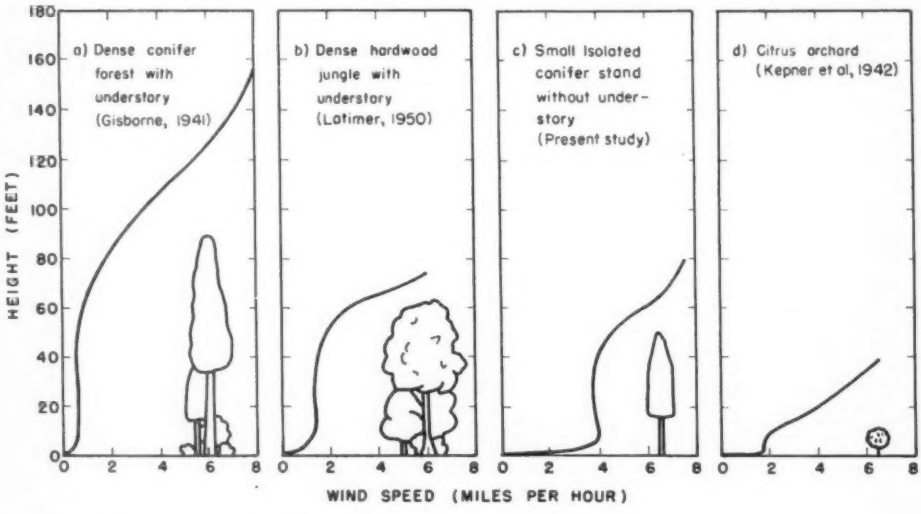
a) Dense conifer forest with understory (Gisborne, 1941)
b) Dense hardwood jungle with understory (Latimer, 1950)
c) Small isolated conifer stand without understory (Present study)
d) Citrus orchard (Kepner et al, 1942)
HEIGHT (FEET)
WIND SPEED (MILES PER HOUR)

FIGURE 7. Comparative wind profiles under inversion conditions.

ditions.

4. Maximum attenuation of wind by tree crowns was 50 to 60 percent during lapse conditions and 60 to 70 percent during inversion conditions. Greater percentage reductions occurred with stronger winds.

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Mikrotopographischer Atlas Mediterraner Hölzer

By Bruno Huber and Christine Rouschal. 107 pp. Fritz Haller Verlag, Berlin-Grunewald. 1954. 28.50 DM. (Approx. $6.78)

REVIEW by Johnson Parker

University of Idaho

Although many Americans may not realize it, a good deal of research was carried out in German universities during World War II which had little or nothing to do with the war effort. Also, with fine precision instruments readily at hand, work in plant anatomy was comparatively easy to undertake. The present book is an outgrowth of some of this wartime research.

Beginning with a gift of Spanish woods to the Tharandt Forestry Academy in 1866, this collection was augmented by the work of Ernst Rouschal around 1936. Although Dr. Rouschal was killed in the war, his wife worked over the collection and together with Bruno Huber, director of the Forest Botany Institute at the University of Munich, made the work ready for publication in 1945. At last, some nine years later, it has been published.

If one opens the book nearly anywhere he finds on the right hand page four photographs, usually of one wood, including cross, radial, and tangential views taken at about 40 to 250 × magnification. On the left is a description of the wood. Also included is a cipher system referring to the punch card method of cataloguing woods. Other interesting details, such as the presence of crystals, are sometimes mentioned.

This book, slim as it is, adds substantially to the microanatomical books on woods such as Eberhard Schmidt's "Mikrotopographische Atlas der mitteleuropäischen Hölzer" (1941), Holdheid's work contained in the "Handbuch der Mikroskopie in der Technik" (1951), Greguss's "Bestimmung der mitteleuropäischen Laubhölzer und Sträucher auf xylotomischer Grundlage" (1945), Metcalfe and Chalk's "Anatomy of the Dicotyledons," and Phillips's "Identification of Softwoods" (1948).

The European Larch: Its Races, Site Requirements and Characteristics

BY
A. L. McCOMB

THE EUROPEAN LARCH (*Larix europaea* D.C.)[1] (*L. decidua* Mill.), from the standpoint of foresters and plant geographers, is one of the most interesting trees of Europe (Rubner, 1952). As early as the middle of the 18th century, when the original central European forests were being cut over, a trend toward increasing use of larch in reforestation was evident. The choice of larch was based on (1) a strong, valuable wood available in large sizes, (2) rapid growth and high yields, and (3) apparent adaptability to a wide variety of sites both in and outside of its natural range. Today, in spite of the failure of many of the original plantations, and partially because of the trend away from pure stands of *Picea excelsa*, larch is recommended as an important component of mixed stands, especially in Germany, Austria and Switzerland.

The purpose of the present paper is to summarize some of the information on larch available in recent European literature, to present some additional data concerning the climate and soils in areas of larch culture in eastern Austria and to review American experience with this species.

The Races of Larch

Larix europaea does not have a continuous range over the European continent (Fig. 1). Instead there are four distinct, closed, natural distribution regions plus several outliers in the east and south Carpathian mountains and the Bihar mountains of Rumania. These groupings of European larch, plus *Larix sibirica* which is native to the northern part of European Russia, and is sometimes considered a sub-species, constitute the larches of Europe.

The four major groups of *Larix europaea* are referred to in the German speaking parts of Europe as (1) Alpen (Alpine), (2) Sudeten, (3) Tatra and (4) Polen (Poland) larch.

The Alpen larch extends throughout the central Alps from southeast France eastward to within about 20 miles of Vienna, Austria. In elevation it occupies a zone extending from timberline, which is 2400 to 2500 meters in the west Alps and 2300 to 2400 meters in the Italian south Tirol, to as low as 300 meters in the Vienna Woods. According to Tschermak (1935) the optimum elevation is 1400 to 1500 meters, yet the larch performs very well at 600-700 meters. Above 1600 meters it is too cold for optimum growth and there are many crooked-stemmed trees.

[1]Nomenclature of European species follows Rubner (1953).

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The area of the Alpen larch, as can be inferred from its horizontal and vertical distribution, does not have a single uniform climate. Larch is most prominent in the interior valleys of the Central Alps which have a continental-type climate. It also occurs in the border mountains of the north Alps having semi-oceanic climates and in the continental-influenced climate of the Vienna Woods. It is most prominent on high ridges and open slopes and generally appears to avoid depressions and valley bottoms.

Although the larch of the Central Alps is often spoken of as the Alpen race of European larch, it lacks the genetic uniformity of a single race. Instead it probably represents a group of races and/or clines. The genetic variability has been demonstrated in Switzerland (Fisher, 1952; Leibundgut and Kunz, 1952), in Austria (Schreiber, 1940) and in Germany (Mormann, 1953; Rubner, 1941; Schober, 1949; Zimmerle, 1941). Rubner (1953) states that at least the larch from the Vienna Woods, the Blühnbach valley and the east Styrian border mountains between 400 and 800 meters elevation must be separated out. His provenance experiments in the Erzgebirge and the forest at Tharandt (Rubner, 1938, 1941) also support the separation of a high elevation race (above 1800 m.) from the low elevation Alpen provenances. Leibundgut and Kunz (1951) tested larch of 27 provenances in the greenhouse, the nursery and at two field locations, in Switzerland. They confirmed the existence of phenologically and morphologically different ecotypes and gave criteria useful in distinguishing among them. Zimmerle (1941) states that the success or failure of larch in Germany depends chiefly on the race used. In Württemberg the low-elevation Alpen sources — Blühnbach and Vienna Woods — are recommended. Mörmann (1953) attributes the generally gratifying success of Alpen larch in Baden to low-and middle-elevation seed sources.

The Sudeten larch is considered by Rubner (1943, 1953) a distinct geographic race (*L. europaea* var. *sudetica*) having special significance for European forestry. The occurrence of this race is limited to the east slope of the Altvater mountains in the southeastern Sudetenland on the present border between Czechosolvakia and Poland. It occurs in stands at elevations between 316 and 850 meters—considerably lower than Alpen larch. Because of snow action it disappears from *Picea excelsa* stands between 700 and 800 meters (Rubner, 1952) and only single specimens reach 1000 meters elevation.

The Sudeten larch (Cieslar, 1914), in comparison to Alpen larch, is faster-growing in youth, more tolerant, straighter in stem, has a narrower crown with thinner, more upward-inclined branches and twigs, and leafs out somewhat later in the spring.

Although Sudeten larch occurs in the transition region between oceanic and continental climates, studies by Rubner (1952) show that differences between Alpen and Sudeten larch cannot be due to climate and that this is a distinct geographical race of the sub-montane region. Unfortunately for accurate racial studies, Alpen larch has been introduced into the Sudetenland and great care must be taken in choosing a seed source.

The Tatra larch, with permanent range in the high and low Tatra mountains of Czechoslovakia and Poland, was investigated thoroughly by Rubner in 1943-44 (1951) and the supposition that its occurrence was related to the impact of a continental climate was confirmed. In the high Tatra larch stands go up to 1500 meters and from this point to timberline single specimens occur with *Picea excelsa* and *Pinus cembra*. In the lower Tatra, larch occurs with *Pinus sylvestris* and other species at 700 to 800 meters. This occurrence with pine on rocky sites at low elevations, along with its occurrence at timberline is characteristic of larch (Rubner, 1952) since it is a shade-intolerant, pioneer species and colonizes naturally open areas laid bare

by avalanches or cultivation, and exceptionally rocky areas. Only through forest management has this natural occurrence pattern been modified.

The Polen larch was originally distributed from upper Silesia through central and southeast Poland. Today there are only a few relict mixed stands, the largest of which lie in the Lysagora (Lyso Gory) region about 60 miles northeast of Krakow, Poland. The Polen larch occurs between 150 and 600 meters elevation. Precipitation in this region (Rubner, 1953) amounts to only 500-550 mm (20-22 inches). It is, therefore, a race of the "plains" with a moderate continental-type climate, as contrasted to the more severe continental climate of the area to the northeast occupied by *Larix sibirica*. Provenance tests of Polen larch have been made in Austria (Schreiber, 1940,1944), and in Württemberg and Tharandt, Germany (Rubner, 1938, 1941), and as a part of the provenance program of the International Union of Forest Research Organizations (Fischer, 1952; Baldwin, 1953).

The most important additional localities of occurrence of *Larix europaea* are in the east Carpathian mountains at Cachlau, Rumania, at an elevation of 1200 to 1400 meters, and in the Bucegi range of the South Carpathian mountains near the Predeal pass.

Another group of larch that deserves comment is the so-called Scottish larch. According to Anderson (1950) the European larch was originally introduced into England in the 16th and into Scotland in the 17th century. Some authorities claim that, more or less by accidental selective breeding, a special race was developed in Perthshire, now known as the Scottish race. This race is very superior in Scotland to some, at least, of the Swiss and Austrian races. Schotte (1916-17) states that the old good larch stands of Sweden came from Scottish sources, while poor stands are of Alpen origin. Rubner (1953) suggests that Scottish larch may be of Sudeten origin.

The question naturally arises whether the larch groups can be differentiated on morphological characteristics. Unfortunately this is not now possible. From a study of 10,000 cones from trees in permanent communities of the four larch groups Rubner (1952, 1953) reports:

1. Alpen larch cones are larger (2 to 3.5 cm. long) than cones from Sudeten (1.8 to 2.8 cm.), Tatra (1.8 to 2.8 cm.) and Polen (1.5 to 2.0 cm.) larches. In the Alps, with several exceptions, the higher the elevation, the larger the cones. The cones of the Vienna Woods larch are larger than the average of each of the four groups.

2. Alpen larch has scales which are weakly arched with a wavy, bent upper edge curved slightly toward the outside; the scales of Tatra, Sudeten and Polen larches, in contrast, are shell-shaped with the upper edge bowed toward the inside.

The above characteristics are not foolproof since weather markedly influences cone size and characteristics, but they are useful in doubtful cases. Fifty to 100 cones, at a minimum, are needed to make a separation.

The first comparative investigation of the growth of larch races was made by Cieslar (1914). This experiment, plus provenance test plantations in Württemberg (Zimmerle, 1941) and Saxony (Rubner, 1952), which are now over 20 years old, show that: (1) the Sudeten larch grows faster than the other three larches. Larch from the Vienna Woods and the Tatra and Polen larches, however, grew nearly as fast. (2) The Alpen larch shows no decrease in average height growth, in relation to source elevation, up to 1600 to 1700 meters. Above 1800 meters there was decreased growth. (3) There are single fast-growing Alpen larch seed sources, e.g. the "Calvalese" from about 1000 meters in the south Alps, the Blühnbachtal at 800 to 1000 meters near Salzburg, and probably the Semmering larch at 1000 meters some 50 miles southwest of Vienna. (4) Tatra

TABLE 1. Climatic data for three larch sites and one larch-free site in Austria.

Place	Elev. (m)	Criterion	Month											
			Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
St. Anton Tirol Austria	1307	Precipitation (mm)	97	70	87	84	74	121	145	145	108	74	76	107	1188
		Temperature (C)	−5.0	−3.9	−0.3	3.5	9.0	12.0	14.0	13.2	10.4	5.4	0.1	−4.0	4.5
		Relative Humidity %	76	72	70	68	68	70	70	74	73	75	77	71	73
		Frost-Free Period	124 days												
Langen Vorarlberg Austria (larch free site)	1220	Precipitation (mm)	155	124	142	166	145	194	222	210	166	120	118	101	1863
		Temperature (C)	−4.8	−2.4	0.1	3.0	8.0	11.2	13.9	13.3	10.5	5.6	1.1	−2.7	4.1
		Relative Humidity %	87	81	81	81	80	81	82	82	82	82	83	83	82
		Frost-Free Period	155 days												
Gutenstein Lower Austria	482	Precipitation (mm)	66	55	61	82	95	116	113	94	91	70	55	68	966
		Temperature (C)	−2.2	−1.1	2.8	6.9	11.9	15.0	16.9	15.6	12.2	7.0	2.2	−0.9	7.3
Ober Hollabrunn Lower Austria	235	Precipitation (mm)	24	20	30	42	62	69	91	60	55	42	26	30	551
		Temperature (C)	−1.6	−0.2	4.2	9.1	14.6	17.6	19.6	18.6	14.8	9.2	3.6	0.0	9.1
		Relative Humidity %	78	74	70	65	65	65	65	67	70	77	80	83	72

Relative Rumidity is average of 7 A.M., 2 P.M. and 9 P.M. readings.

and Sudeten larch in comparison to Alpen larch, show no growth differences associated with elevation of seed source.

The International Union of Forest Research Organizations has sponsored larch provenance tests in Europe and America. Based on eight years growth Fisher (1952) tentatively recommends the following five provenances for the Swiss midlands: Blühnbach and Krumbach from Austria, Cierny and Murau from the Tatra and Hubertskirch from Sudetenland. All are how-elevation provenances.

Leibundgut and Kunz (1952) list the following characters as useful in distinguishing larch of different provenances:

1. The yearly course of height growth. They found that the growth of Alpen larch from high elevation took place early, in contrast to Sudeten and low-elevation Alpen provenances. The time in which half the height growth was completed was most useful; some seed sources differed by as much as a month.

2. Total height of 6-8 year old larches. Height tended to decrease with increasing elevation, although there were numerous exceptions. Alpen larch from low elevations attained nearly the same height as Sudeten larch.

3. High-elevation provenances turned color earlier in fall and exhibited greater branch thickness.

Schreiber (1944) found that Polen larch had the thickest, and Sudeten larch the thinnest, bark. Heartwood formation in 25-year-old larch was greatest in Sudeten and least in Alpen larch.

Distribution and Occurrence in Relation to Climate

The Alpen larch is found naturally at elevations whose average temperature relations give rise to beech (*Fagus sylvatica*) at lower elevations, and spruce (*Picea excelsa*) at higher elevations. Within these elevational zones there is great variation in the abundance of larch.

Largely as a result of the studies of Tschermak (1935) the natural distribution of European larch (Alpen group) is considered related to the occurrence of a continental-type climate. Tschermak's map shows great concentration of larch in the interior Alpine valleys. On the northern rim of the Alps and at other locations where there is little or no larch, the sites are open to the moist winds from the Atlantic ocean. Frequently one and the same mountain chain is free of larch on its windward side and colonized by larch on its lee side. This relationship is vividly demonstrated when one journeys from the Boden See, at the German-Swiss-Austrian border, through Vorarlberg and over the Arlberg pass into Tirol, Austria. On the northwest edge of the Alps there is much beech and practically no larch; in Vorarlberg there is a scattered occurrence of larch; but over the pass in Tirol beech all but disappears and is replaced predominantly by larch. Vorarlberg and the nearby, low-lying areas of Germany and Switzerland are open to the incoming, moisture-bearing winds from the west and have a distinct oceanic-type climate. In contrast, Tirol is blocked on the north, west and south from these winds which lose most of their moisture on the outer slopes and are warmed and become drier as they descend into the interior valleys.

Table 1, giving climatic data for three larch areas in Austria, contrasts the climate for St. Anton in Tirol (larch-abundant site) with Langen in Vorarlberg (larch-free site) and illustrates the above relationship. Both stations are at about the same elevation yet Langen receives 67 percent more precipitation than St. Anton and the relative humidity averages 10 percent more (15% during mid-day). While the average annual temperatures are similar, St. Anton is warmer in summer and colder in the winter, and the average daily temperature fluctuates over a wider range. Tschermak (1935) cites many instances of the above relationship in the eastern Alps, both north and south of the higher Alpine masses.

Larch has other peculiarities of distribution worth noting. On the chief mountain ridges larch is more abundant on the south than on the north sides. As one travels from the outer to the inner Alps, at a given elevation, the larch stocking percentage increases. In the interior valleys the timberline lies higher than on the outside ridges and the percentage of larch increases with increasing elevation. In all of these cases the relatively larch-free sites have less fluctuating temperatures and are cloudier than the larch-abundant sites.

The influence of continental climate on larch is further illustrated by contrasting larch abundance in the northern border mountains of the Alps. West from Steyer, Austria thru Vorarlberg and Switzerland the outside Alpine ranges are generally avoided by larch. Eastward in Lower Austria and southeastward in Steiermark, however, the lowest border mountains are colonized by larch which appears to prefer the shady mountain sides. Table 1 gives climatic data for Gutenstein, Lower Austria at the extreme eastward extension of Alpen larch, and for Ober Hollabrunn in the rolling to hilly land 50 miles north of Vienna, where introduced larch thrives. The climate here is transitional from oceanic to continental and both sites have higher temperatures, greater temperature fluctuation and lower relative humidity than border or mountain areas to the west.

In the area of the Alps and over the entire natural range of the species, larch is found thriving on a great variety of sites differing with respect to elevation, aspect, radiation, temperature, precipitation, humidity and length of growing season. These sites, according to Rubner (1952) and Tschermak (1935) have one thing in common—a continental-type climate with relatively great temperature variation and

FIGURE 1. Distribution of the major naturally-occurring groups of European larch.

TABLE 2. Climatic data for different areas of larch culture and occurrence. (After Schober, 1949)

Site Class	Location	Growing season		Precipitation-mm		Rain Factor
		Tempera-ture-C	Precipi-tation-mm	Dormant Season	Annual	
I-II	Northwest Germany	14.6	2.31	1.79	731	15.8
III-V	Northwest Germany	14.6	2.18	1.69	693	14.9
I-II	Baden	14.8	2.7	2.0	829	18.2
I-II	Württemberg	15.6	2.8	1.8	812	17.9
	Sudeten larch (400 m. elev.)	14.1	2.3		657	16.5
	Alpen larch Tauern (750 m. elev.)	13.6	3.5		1059	26.0
	Polen larch Lemberg, Krakau (275 m. elev.)	16.0	2.4		812	15.0

Precipitation for growing and dormant seasons given in millimeters per day.

$$\text{Rain factor} = \frac{\text{Ave. growing season temperature}}{\text{Ave. daily growing season precipitation}} \times 100.$$

summer days with much incoming and outgoing radiation.

In the areas of west Germany and Switzerland, where larch has been artificially introduced, the climate is oceanic instead of continental. Schober (1949), who studied 127 larch stands in northwest Germany, many of which were of high vigor, states that apparently larch is not bound to a continental climate or to a particular level of temperature and precipitation. Lang (1932) states that the relative terms "continental" and "oceanic" should not be used, that larch grows well both in the mountains and on level lowlands and that a light-filled space is its principal site requirement. Table 2 gives climatic data for areas of larch cultivation in Germany as contrasted to areas of the Sudeten, Alpen and Polen larches.

Although the sites of abundant natural larch occurrence receive less precipitation than sites without larch, the best larch sites are in no way precipitation-poor. Larch has a high transpiration ratio (water requirement), according to Tschermak (1935) and Schreiber (1921), and would not be expected to thrive on dry sites.[2] Great transpiration assumes an abundant water supply. Therefore, according to one common European view, larch prefers moist sites with considerable clear weather, intense incoming radiation, higher day temperatures and wind movement. Tschermak, the principal proponent of this view, states that light relations, as such, play no role in the natural distribution of Alpen larch.

Münch (1936) does not agree on the importance of temperature flunctuations and high transpiration, and Bühler (1922) and Lang (1932) accepted light as a factor playing an important part in the distribution of larch.

In view of the many excellent larch stands in west Germany (Mörmann, 1953; Schober, 1949; Zimmerle, 1941) the present author doubts that the conditions for

[2]Burger (1945) states that larch has the highest water requirement of any of the common European conifers.

FIGURE 2. Mature larch stand in the Albula valley, Switzerland (Courtesy Eidg. Anstalt für das forstliche Versuchswesen, Switzerland).

FIGURE 3. Larch in the Oberhallstein valley, Switzerland (courtesy Eidg. Anstalt für das forstliche Versuchswesen, Switzerland).

rapid transpiration determine the local occurrence and abundance of larch. European larch is said to be less intolerant of shade at high elevations, where there is more incoming radiation and generally more larch. Light itself (Lang, 1932), or light in connection with temperature, particularly as they affect the course of competition, could be determinative. Rubner (1953), however, states that the natural boundaries of larch cannot be thought of as due only to competition since there are, in the region of larch outposts, numerous old avalanche strips where competition with other species is excluded, but which are not colonized by larch.

Soil Requirements and Tolerances

In Switzerland, because it did not occur in the northern and western border mountains, which were formed predominantly of limestones and dolomites, larch was previously considered a calcophobic species. In contrast, in Germany, because larch seemed to grow better on limestone-derived soils it was once considered calcophilic. Studies by Tschermak (1935) in Austria, Zimmerle (1941) in Württemberg and Mörmann (1953) in Baden show that larch grows satisfactorily on soils derived from many different types of rocks and that the distributional boundaries of larch are not influenced by the underlying rock type.

The relations of larch occurrence and growth to soil have been investigated in Germany, Austria and the United States (Aird and Stone, 1955). Tschermak (1935) and Lang (1932) concluded that, like most tree species, larch grows best on

average to deep, loose, fresh loam and sandy loam soils. It does not thrive on tight loam soils especially in rainfall-rich regions. Zimmerle (1941) reported detailed profile descriptions and soil analyses for a number of larch sites in Württemberg. Pore volumes, water and air content, water at field capacity, capillary water rise, exchangeable bases and pH were investigated. Results of this investigation did not support the earlier assumption of Lang (1932) that larch in warm regions grows best on acid, nutrient-poor soil. No connection was found between larch growth and vigor and either pH or exchangeable bases; larch was found on site quality I on strongly acid, weakly acid and neutral soils. Soils of site quality I were characterized by greater than average depth, good water conduction, field capacity usually under 30 percent by volume, air content sufficient for root respiration and penetration of roots throughout the different horizons. The physical soil properties, and not soil fertility and reaction, thus have a decisive influence on the growth of larch on most sites. Anderson (1950), however, states that larch requires at least moderate base-richness and fails on infertile soil; and that larch is not "happy" on extremely base-rich sites.

That larch is a species favored by moist, fresh soil in supported by the following evidence: On dry, sunny slopes the larch stocking percentage tends to be very small; on very shallow soils larch is short-shafted and narrow-ringed. Larch favors the shady north aspects, particularly in the dry, steep-sloped dolomite mountains, on warm, low-elevation sites, in valleys subjected to the action of the dessicating Föhn[3] winds, and at the low elevations of the long, central Alps valleys which receive small amounts of precipitation.

European larch is sensitive to soil wetness resulting from poor surface and internal drainage. Tschermak (1935) noted that larches planted on wet meadow showed poor growth-form, were covered with lichens from top to bottom, had low-vigor crowns and were gradually dying. Cieslar (1904) reported a similar example where, after 20 to 30 years, many trees had died, those remaining were mostly spike-topped and there was severe infection with larch canker. Bühler (1922) describes 18-year-old larch on impermeable subsoil in a research garden at Tübingen, Germany as covered with lichens while on drained ground they were free of lichens. In still another example (Tschermak, 1935), 8 foot-high chlorotic larch on undrained soil regained normal green color one year after drainage.

Larch also appears sensitive to soil compaction. Tschermak (1935) notes that conifers planted on land previously used for agriculture often die after a period of good growth. His explanation is that soil freed of stones and decaying tree roots takes on a very dense structure. Two examples were noted within the natural range of larch, one where larch was planted alone, the second where larch and spruce were planted together. In the latter larch proved more sensitive than spruce to soil compaction. In a third example outside the natural range of larch several thousand trees thrived for 20 years on former agricultural land, later sickened and died. The sensitivity of larch to poor soil drainage and compaction suggests that the roots have either high oxygen requirements, low carbon dioxide tolerance, or both.

European larch is one of several European conifers, including *Pinus nigra austriaca*, *Pinus sylvestris*, and *Picea excelsa*, that remain healthy and can make satisfactory growth on natural, highly calcareous soils. Zimmerle (1941) found larch in Württemberg thriving both on strongly acid (pH 4.3) and near neutral soils. In the eastern Alps Tschermak (1935) found that larch thrived on acid, neutral and strongly alkaline soils. Table 3, giving supporting data, shows that dominant larches

[3]A chinook-type wind becoming warmer and drier as it descends after passing over Alpine crests.

TABLE 3. Larch occurrence and growth in relation to geologic formation and soil pH (adapted from Tschermak, 1935)

Geological Formation	Elevation meters	Age years	Total Height meters	pH Depth of soil Sample 5-10 cm	20-25 cm	45-50 cm	Associated Species
Limestone	....	....	35	7.2	7.3	7.3	Spruce, Fir, Beech
Shale with limestone	570	50	19	7.4	7.2	7.3	Scotch pine
Limestone	600	....	....	7.3	....	7.3	Unknown
Limestone	....	73	27	7.0	7.7	7.7	Spruce, Beech
Flysch and sandstone	740	120	36	5.5	5.1	5.3	Beech, fir
Limestone	1,000	150	20	5.6	7.9	8.3	Unknown
Limey, dolomitic shale (Slate)	1,000	110	35	8.7	8.6	8.8	Spruce, Beech
Mica schist	1,360	140	....	7.4	7.5	7.6	Unknown
Slate (shale)	1,500	100	26	5.0	6.9	6.8	Spruce

35 meters (115 feet) high were found on soils, derived from sandstone and flysch, with pH values of 5.1 to 5.6 and also on soils formed from calcareous, dolomitic shales with pH values up to 8.6 and 8.8.[4]

This author has investigated larch growing at the edge of, and beyond its natural range, in eastern Austria, in an area where precipitation varies from 550 to 900 mm (22 to 36 inches) annually. Thrifty larch was found on five sites where the pH at the surface and throughout the entire profile was 7.6 and above. Three of the five sites were extremely dry. The soils investigated were formed from calcareous conglomerate, loess, and sandy gravel, respectively. Table 4 contains data relating to two of the alkaline- and one of the acid-soil sites. From all of these data it can be concluded that larch is capable of growing on the most alkaline of naturally calcareous soils, as well as on quite strongly acid soils.

The Larch Canker

The European larch in its permanent range in the east Alps is an exceptionally resistant, tenacious, healthy species (Tschermak, 1935). However, when the range of larch was extended by planting and seeding, particularly into the lowlands of Germany, a serious larch disease became evident. This disease, the larch canker, is caused by the fungus *Dasycypha willkommii* (Hart) Rehm.

The entire larch culture in Germany is dominated by the question of the larch sickness, which is a very complex phenomenon (Rubner, 1952) (Forestry Commission Gt. Britain, 1948). Generally the first symptom of the disease is the dying of branches, starting at the base of the crown and working upwards ("aufsteigenden Zweigdürre"). Frequently the lower part of the stem and the lower branches are covered with lichens. The larch canker fungus is connected, in some manner not yet entirely clear, with the branch dying.

Since the larch canker is most prevalent in the mild climate regions of the German lowlands, Münch (1936) and Day (1931, 1951, 1955) see its cause in the early beginning of vegetative growth and in late spring frost damage. The disease generally does not manifest itself until after the first 10 to 15 years and is most serious between the 20th and 40th (Rubner, 1952) or 20th and 80th years (Schober, 1949).

[4]Since the pH at equilibrium, of a soil solution saturated with calcium carbonate, is about 8.3, Tschermak's pH values of 8.6 to 8.8 are evidently due to the presence of considerable Mg or other ions.

Why the branch dying and canker infection begins after the larch has outgrown the frost zone is not known and Burger (1945) cites this as evidence against the frost theory.

Langner (1936) states that the canker fungus cannot grow through healthy bark tissue during the growing season. It is limited at the end of the vegetative period, to a several millimeter-broad branch zone where, due to enzyme action and tannin deposition, the osmotic pressure of the cells has been reduced. These cells freeze with a very light frost and with warmer weather the fungus penetrates the frozen tissue. A new zone of tissue is then in a like manner made frost-sensitive. This process may be repeated several times during a warm winter. The more longitudinal form of the canker is due to severe drying of infected tissue in summer, followed by cork formation and the separation of healthy and diseased tissue by a split over which the fungus cannot bridge itself.

According to Plassmann (1927) *Dasycypha willkommii* occurs both as a saphrophyte and a parasite on larch. It may first infect dead branches and then spread to living tissues. Because it occurs as a saphrophyte, spores are available each year in almost every stand for parasitic infection. Avoidance of pure stands, therefore, as recommended in some texts, is not a satisfactory control measure. Useful control measures are (1) pruning of dead branches before the fungus has an opportunity to infect the main stem, and (2) postponing natural pruning until the beginning of strong bark formation at about 20 years of age.

TABLE 4. Profile description and pH for three loess-derived soils supporting larch in northeastern Austria. Precipitation 600 mm (24 inches) annually.

Location	Horizon	Depth Through Horizon *cm*	pH[1] and Depth	Tree and Site Description
				Aspect ..... SSW
	A_1	15	5.8 @ 3 cm	Slope ..... 28 percent
I	A_3	36	4.8 @ 32 cm	Age dominant larch ..... 58 years
	B	78	5.2 @ 56 cm	Height dominant larch 70 feet
	C	100 +	5.4 @ 95 cm	Associated species ..... *Pinus sylvestris*
				Picea excelsa
				Quercus sessiliflora
				Aspect ..... Valley
				Slope ..... None
II	A_1	23	7.6 @ 3 cm	Age dominant larch ..... 109 years
	C_1	53	8.2 @ 50 cm	Height dominant larch 95 feet
	C	100 +	7.8 @ 95 cm	Associated species ..... *Pinus sylvestris*
				Picea excelsa
				Aspect ..... SE
	A_1	40	7.9 @ 3 cm	Slope ..... 25 percent
III	A_3 / C_1	70	8.3 @ 60 cm	Age dominant larch ..... 20 years
				Height dominant larch 20 feet
	C	100 +		Associated species ..... *Corylus* sp.
				Cornus sp.
				Crataegus sp.

[1]pH values determined with glass electrode.

During the 18th century very much larch was planted in Germany. Had the plantations all succeeded larch would today make up 30 percent of the stocking in stands in German forests (Rubner, 1952). By the middle of the 19th century a reaction against further planting of larch had set in. But in spite of the canker, and because of the fast growth of larch in youth and the production of excellent wood, it continued to be planted. In the long run most of the plantations failed but a few did not become infected with canker. The presence of these thriving plantations in the same localities with seriously cankered larch was spoken of as the larch puzzle (lärchenrätzel).

In south Bavaria, outside the Alps, only a few small good stands of larch exist. In northern Bavaria and in northwestern Germany, good stands occur more frequently. In Baden, by contrast, (Mörmann, 1953) larch has grown quite satisfactorily. Investigation of the good and poor larch stands in Braunschweig (Germany) has shown that the high quality 130 year-old stands grew from seed collected in the Sudetenland, while the severely-cankered 60-80 year-old stands are of Alpen origin. Mörmann (1953) has traced the many canker-free larch stands of Baden, Germany, to seed from low elevation Alpen sources. The excellent larch stands in Schlitz in Hessen are thought to have originated either from the Vienna Woods or from low-elevation Alpen sources.

Cieslar (1914) could not prove that Sudeten larch was more canker-free than Alpen larch because young Sudetenland larch stands, from which seeds were obtained, often originated from Alpen sources. Münch (1936), however, was later able to prove that the cankerless stands were composed of genuine Sudeten larch. The experiments in Württemberg, Germany, now over 20 years old, show (Zimmerle, 1941; Rubner, 1952) that Sudeten, Tatra and Vienna Woods larch are completely or almost canker free, while Alpen larch, in this oceanic-influenced climate, is very seriously infected. Japanese and Korean larch are also canker-free. Rübner (1952), who is very familiar with Sudeten larch stands and has traveled widely in the Tatra and Vienna Woods areas, states that larch canker is very rarely encountered among trees of these three races in their native habitats.

Compared to Sudeten larch, Alpen larch, at least of some provenances, starts shoot growth 5 to 8 days earlier in the spring (Münch, 1936), and is therefore often endangered by frost. Bark, cambium and buds are damaged and made susceptible to canker-fungus infection. Burger (1935) has shown, and Leibundgut and Kunz (1952) have confirmed, that Alpen larch from high-elevation sites starts growth earlier than that from low elevations.

Rubner (1953) states there is more larch canker at high elevations in the Alps than at low elevations and he quotes Cieslar as saying canker is more abundant where the life functions of the tree were most disturbed by mechanical interference. Burger (1943) suggests that where fungi and insects attack larch needles the new shoot growth does not completely ripen in the fall and is more susceptible to frost and canker.

Schober (1949) does not agree that the canker problem is primarily a problem of race. As proof he states that, of the larch stands of Alpen origin in northwest Germany, those over 90 years of age are canker-free while 54 percent of the younger stands have 10 percent or more of infected stems. Schober emphasizes that the immunity of Sudeten and the susceptibility of Alpen larch to canker are not proven and that a widespread use of Sudeten larch as insurance against canker loss is poor policy. Rubner (1952) believes that Schober's older larch were of low elevation Alpen provenance.

While the preponderance of evidence suggests that the larch canker in the low-lying, oceanic-influenced climate areas of

FIGURE 4. Larch-broadleaf mixture in Forstamt Neckarschwarzach, Baden, Germany. Largest trees are 37 meters (122 feet) high and 86 cm. (34 inches) in diameter. (Courtesy Forstmeister E. Sauer and Oberforstmeister P. Mörmann).

Europe is primarily a problem of race, most authors agree that much can be done in minimizing canker infection through careful site selection, timely thinning and silvicultural treatment designed to maintain rapid growth. Many foresters consider the latter of equal importance to proper race.

Other Enemies of Larch

The following summary of some of the agencies injurious to larch is taken from Tschermak (1935) and (Mörmann (1953). It should be emphasized that larch is an exceptionally pest-free and resistant species in its natural range.

On steep slopes larch develops bent stems (säbelwuchs) due to snow and soil movement down slope. Larch suffers rather serious snow breakage and stem bending, especially where heavy wet snows occur; it is resistant to fall and winter frost but is somewhat more sensitive to spring frosts. Larch is more frequently damaged by lightning than associated species which it generally overtops. It is superior to all associated species in resistance to windthrow.

Larch is injured by deer, squirrels and mice. Young trees are damaged or killed through rubbing and biting by the small roe-deer (reh) as well as occasionally by the large red deer (hirsch). Mörmann lists deer as the most serious enemy of larch in Baden, Germany. In one instance 56,000 out of 72,000 plants were lost. Squirrels peel and girdle young larch, especially the top one-half meter of stem. On grassy sites, especially in mild climates, mice may cause serious damage by chewing the tender bark in winter.

The principal insects causing damage are the larch case bearer (*Coleophora laricella* Hbn.), the larch shoot moth (*Argyresthia laevigatella* H. Sch.), the larch leaf roller (*Grapholita diviana* Gn. and the "lärchen-

FIGURE 5. An eighty-year-old European larch plantation on deep silt-loam soil in central Iowa. Area used by both sheep and hogs. Dominant trees 75-80 feet tall.

rindenwicklers" (*Grapholita zebeana* Rtzb.), the eight-toothed larch bark beetle (*Ips cembrae* Heer), the bark beetle (*Tetropium Gabrieli* Weise), the larch bud gall midge (*Cecidomya Kellneri* Hnschl.), several aphids (*Chermes abietis* L.) and (*Chermes strobilobius* Klth.), the larch cone and seed fly (*Chortophila laricicola* Karl) and the larch thrips (*Taeniothrips laricivorus* Krat.).

Besides the canker fungus the principal fungus enemies of larch are the butt rots caused by *Fomes annosus* (Fr.) Cke. and *Polyporus schweinitzii* Fr., the larch needle rust (*Melampsora larici-tremulae* Kleb.) and a needle blight fungus (*Hypodermella laricis* v. Tub.).

Requirements for Mixed Stands

The two most important natural mixed types of the eastern Alps, of which larch is an important component, are (Tschermak, 1935): (1) Spruce-Fir-Larch-Beech (*Picea excelsa, Abies pectinata, Larix europaea, Fagus sylvatica*) with or without *Pinus sylvestris*; and (2) Spruce-Larch (Leibundgut, 1951). The first occurs in the border ranges of the Alps north and south of the highest summits, the latter is the principal type of the inner Alpine valleys. Larch occurs naturally and has been widely cultured in other types.

Hardly any other tree in Europe possesses so many valuable qualities, making it suited as a component of mixed stands, as does the larch. Schober (1949 and 1952) and others list the following as characteristics affecting its use in mixed stands.

1. Larch produces superior, valuable timbers and, through its mixture with pine and beech, total yields are greater than are often obtainable with the same species grown in pure stands.

2. Larch, up to the age of 30 to 40 years, will outgrow in height all other commonly-used European upland species. If given full light from the start, larch remains a head dominant for many years and by later careful thinning it can be maintained in stands until the rotation end.

3. Larch is very shade-intolerant and where crowns touch the larch is easily suppressed by other species; only its fast growth in full light or timely thinning will result in its retention in the stand.

4. Larch has great longevity and attains considerable height on good sites. Tschermak found larches in Tirol, Austria, up to 672 years of age and heights up to 47 meters (155 feet). Entire stands up to 150 years of age are common at middle elevations and between 150 and 250 years at higher elevations. Mörmann (1953) cites the case of a larch planted in Baden, Germany in 1791 which in 1950 was 56 meters (184 feet) high. Larch can live in most mixed stands as long as any other species in the mixture; this is in distinct contrast to *Picea excelsa* which on lowland sites is managed on an 80 to 100 year rotation and does not commonly come through on the longer rotations used for beech, pine and oak. The attaining of great heights also helps the very intolerant larch in competing and maintaining itself in mixed stands.

5. Larch, because of its deep rooting habit, is normally very windfirm on all except very shallow or poorly-drained, compacted soils.

6. When larch is used with beech, larch can be held over, after the beech has been regenerated, for the purpose of seeding openings to larch. In such cases the beech reproduction is not damaged by shading and competition, and epicormic branch formation on the larch is not abundant.

7. Larch (Schober, 1952), when used with tolerant species, can improve soil conditions. In 116 pure and mixed larch stands investigated in northwestern Germany Schober (1952) seldom observed raw-humus formation. A fairly rapid and complete decomposition of litter and humus is favored by the easy passage of light through older larch stands and by other altered stand climatic factors. Other investigators (Bungert, 1935; Wittich, 1933) have cited examples of raw humus formation under larch and of the difficulty of decomposing larch litter.

8. On most sites, in mixture with beech, larch has smaller, finer branches than *Pinus sylvestris*, which is often poor-formed.

The failure of larch in Germany, besides its use on unsuited sites had been due to (1) the larch canker and (2) strong competition with tolerant species, like beech or spruce, when timely thinnings were not made. Larch should be limited to the better sites because it more quickly grows through the size classes subject to canker infection.

The most common artificial mixtures with larch are spruce-larch, beech-larch, oak-larch, pine-larch. In west Germany (Schober, 1949); Mörmann, 1953) the mixture spruce-larch is not favored because spruce competes too strongly for crown space and provides a better stand climate for growth of the larch canker fungus. Lichen formation is also encouraged. This is in contrast to the situation in the Alpen and Sudeten homes of the larch where there is a more natural mixture of these two species.

The mixture beech-larch is very promising. Where this mixture has failed in the past the principal cause was failure to thin at the correct times to maintain the dominance of the larch. This mixture is very successful if beech is established somewhat later than the larch. Schober (1952) cites examples of superior beech-larch mixtures where the larch is 30 to 52 years older than the 60 to 70 year old beech with which it is mixed. Timely thinning is especially important on the good larch sites which are also good beech sites. In northwest Germany there were fewer canker-infected larch stems in larch-beech mixtures than in pine-larch stands (Schober, 1949).

The mixture oak-larch appears very promising (Schober, 1949 and 1952) but on average oak sites there is danger that the oak will be overgrown by the faster-growing larch and will become an understory tree, in which position it is not vigorous. Larch in such stands is often very limby. On the best oak sites a larger part of the oaks can be maintained in the dominant and codominant classes. A disadvantage is that oak requires a very long rotation to attain the most valuable sizes and in these cases larch, in Germany, frequently becomes rotted at the butt. The rot is caused mostly by *Fomes annosus* and less often by *Polyporus schweinitzii*. Dominant as well as intermediate trees are infected

The mixture pine-larch can be recommended only where there is sufficient soil freshness for the larch. On typical pine sites with dry soils, little precipitation or low water tables, the larch grows more slowly than the pine and this mixture is not recommended. Larch has its principal value in large sizes which are produced only on the better sites (Mörmann, 1953).

The mixture beech-oak-larch is very promising in Baden, Germany, but timely thinnings are needed to keep the larch in the head dominant position. The mixture beech-oak-pine-larch, common in Baden, is also very promising.

Schober (1952) states that successful larch mixtures are attainable on sites with deep, fresh, loamy to clayey soil with excellent water-supplying characteristics. Other factors favoring successful larch mixtures are careful choice of the method of forming or regenerating the stands, the kind of mixture and stand care, especially timely thinning. In Baden, Germany, beech-oak-larch-pine is frequently regenerated naturally by some form of progressive strip shelterwood method.

European Larch in the United States

Following the Civil War, larch was planted sporadically in Massachusetts, Connecticut and Vermont (Hunt, 1932; Cook, 1939) and rather widely as windbreaks and woodlots, particularly in the western part of the Corn Belt. Younger plantations are most numerous in Pennsylvania, New York and southern New England. The availability of planting stock from Europe, at a time when nursery stock of American species was unavailable, was the principal

reason for the early American plantations of larch, Scotch pine and Norway spruce (Baldwin, 1953). The excellent performance of larch on suited sites suggests that this species will find wider use in northeastern and north central United States. In addition to its use as a construction timber and for poles, ties and posts, larch can be pulped (Cook, 1947) and the oleoresin used for preparation of Venetian turpentine (Tschermak, 1935).

The provenances of the older larch plantations are not accurately known. Cook (1939) and Hunt (1932) cite opinion and evidence that most of the older larch in New England is of Scottish or English origin. Baldwin (1953) suggests that much of the coniferous planting stock used in the nineteenth century was imported from Germany or Holland. Larch imported from Germany likely would be of the high and low Alpen and Sudeten races.

Seed origin for many of the more recent larch plantations is better known (Baldwin, 1953; Cook, 1941, 1942; Littlefield and Eliason, 1953). As a part of the larch provenance testing program of the International Union of Forest Research Organizations, Baldwin (1953) received 55 lots of seed from Europe in 1946. These were planted in New York and New Hampshire and plantations established in 1948. Other provenance tests are in progress in four additional localities (Wright, 1955). Some of these include comparative tests of Japanese larch, *Larix leptolepis* Sieb. and Zucc., the Dunkeld hybrid larch, *Larix eurolepis* (*Larix europaea* × *L. leptolepis*) and the Dahurian larch, *Larix gmelini* Rupr. Litvin.

European larch in America exhibits the rapid height growth characteristic of the species in Europe (Cook, 1946). Hunt (1932), from a study of 47 sample plots in New England and New York, and Aird and Stone (1955) from 45 plots, found site index values ranging from 35 to 85. On site index 80 heights of 65 feet are attained in 30 years. In Iowa deep silt-loam soils of the Fayette series on exposed sites support trees 80 to 95 feet tall, heights superior by 5 to 15 feet to those attained by adjacent hardwoods.

In duration of height growth, larch behaves more like hardwoods than conifers. Cook (1941) found that larch started growth in New York between May 27 and June 4 and stopped between August 30 and September 23. The period of height growth averaged 99 days. Corresponding periods in days for other conifers were: red pine—54, American larch—88, red spruce—61, white spruce—59, Norway spruce—48 and hemlock—85. The longer period of height growth may explain the greater yearly growth of larch.

Diameter growth is also very rapid in youth but decreases quickly in unthinned stands, indicating need of early thinning. In a 15-year-old plantation (Cook, 1946), where the average diameter of all trees was 4.4 inches, the largest tree was 6.9 inches B.H. and 49 feet tall and the average height of all dominant trees was 40 feet. In unthinned stands at 60 years on site class I yields are about 5500 cubic feet per acre and on site class III about 4,000 cubic feet (Hunt, 1932).

Studies in the U.S., like those in Europe, show that larch prefers a deep, well-drained soil in the texture range fine-sandy-loam through silt-loam (Hunt, 1932; Aird and Stone, 1955). It does not grow well on excessively drained soils nor on stiff clays and is sensitive to poor soil drainage as indicated by gley development, mottling and compaction (Aird and Stone, 1955). Although there is some evidence to the contrary (Day, 1948), observations in Iowa and Europe show larch capable of growing on highly calcareous soils wtih pH values well in the alkaline range.

Larch is resistant to winter cold and is not subject to winter killing (Hunt, 1932), an important point in its favor when larch is planted in the western half of the Corn Belt. Larch often suffers from late spring frost, causing young trees to become bushy, a condition which they later outgrow (Hunt, 1932). Buds burst very early, often

before the frost is out of the ground, and leaves are fully grown before shoot growth begins (Cook, 1941). Survival of larch planting stock in Iowa is low if buds burst while stock is in transit or before planting. Lang (1937) attributes such planting losses to the fact that new root growth does not immediately follow bud burst. The supply of water for new foliage must come from the old root system and this supply is often inadequate if there is incomplete soil-root contact or if new foliage is subjected to intense radiation, low humidity and high winds. Early bud burst makes larch particularly susceptible to injury in frost pockets.

Larch suffers injury from numerous other sources. Twenty-five percent of the plantations surveyed by Hunt (1932) had been noticeably injured by ice storms, the branches and leaders of larch being rather brittle. Red squirrels (*Sciurus hudsonicus*) cause considerable damage locally by cutting off twigs to get the buds on which they feed (Hunt, 1932; Cook, 1954). Sudeten larch appeared to be less susceptible than Scottish larch (Cook, 1954). Porcupines (*Erethizon dorsatum dorsatum*), by eating the inner bark and girdling the tree, cause more serious injury to larch than squirrels and were the principal reason for discontinuing the planting of this species on the Harvard Forest (Spurr, 1950). The animals may work at any height but usually the girdling is near the top where the bark is still smooth and tender (Hunt, 1932).

The principal fungal enemies of European larch are *Fomes annosus*, which causes a butt rot, and *Dasyscypha willkommii*, the larch canker fungus (Hunt, 1932). The latter was first discovered in America in 1927.

Insects found feeding on European larch in the U.S. are the larch sawfly (*Pristiphora erichsonii* Htg.), which was first definitely recorded in North America in 1882, but which may be native to both America and Europe (Craighead, 1950; Hunt, 1932), the larch case bearer (*Coleophora laricella* Hbn.), which is native to Europe but is found in the U.S. (Craighead, 1950; Hunt, 1932) and several species of aphids, particularly *Chermes strobilobius* Kalt. which has been found in northeastern U.S. (Hunt, 1932).

In planting European larch in the Northeast, 2- or 3-year-old planting stock of sufficient size to protrude above grass is preferred (Hunt, 1932). Fall planting is recommended because of the early spring bud burst and subsequent frost injury, October being the preferred month. Hunt (1932) recommends a spacing of 7 to 8 feet and suggests that stands mixed with hardwoods will be safer and more profitable in the long run.

Plantations set out on cutover lands or brushy old-fields require weeding during the first 10 to 12 years (Hunt, 1932; Cook, 1955). Because of the extreme intolerance of the species weeding should start early. Once dominant the larch will outgrow all other conifers commonly used in the East, except possibly Norway spruce (Hosley, 1936). Hunt (1932) suggests that thinnings should begin early, at about 20 years for a seven foot spacing and perhaps 25 years for 8 foot spacing. Observations in Iowa point to the desirability of even earlier thinning as is recommended in Great Britain.

Discussion and Summary

The European larch extends from southeastern France to east central Rumania and north to central Poland; in elevation it ranges from timberline at 2500 meters (8200 ft.) in the central Alps to about 150 meters (500 feet) in Poland. Within this area are four separate major distributional groups — The Alpen, Sudeten, Tatra and Polen—plus several smaller outliers in Rumania. Between and within some of these groupings are major genetic differences of importance in the culture of larch.

In the Alpen group there are major differences in growth, time of shoot formation and canker susceptibility associated with elevation of origin. The Sudeten larch starts shoot growth 5 to 8 days later

than many of the Alpen provenances, is more canker-free at low elevations and is considered a distinct race (*Larix europaea sudetica*). Only a few remnants of the once widely distributed Polen larch now exist. This group and the Tatra larch, although less thoroughly investigated than the Alpen and Sudeten groups, are considered distinct racial groups which differ from each other and from Sudeten and Alpen larches. Attempts to differentiate between the groups on a morphological basis have proven only moderately successful. Certain growth characteristics have proven useful in distinguishing high from low elevation provenances within the Alpen group.

The principal European larch disease, and one very important in larch culture in the lowlands of west Europe, is the larch canker caused by the fungus *Dasycypha willkommii*. Larch, in the regions of its natural occurrence, is a very healthy, resistant, long-lived species. However, when planted in the low-lying areas of west and northwest Germany, most of the trees became infected with canker fungus and died. The presence of a few healthy plantations among others which completely failed was referred to as the larch puzzle. Differences in canker infection were later traced to differences in seed provenance. Sudeten, Tatra and Polen larches, as well as at least some of the low-elevation Alpen larches are resistant to larch canker. Several of the better low-elevation Alpen sources are Blühnbachtal, Vienna Woods, and Semmering. The higher elevation provenances, when planted in the lowlands with oceanic climate, were seriously canker-infected. The apparent cause lies in the earlier starting of shoot growth coupled with late spring frost which opens the damaged tissue to fungus infection.

The larch is a long-lived, fast-growing tree that produces a valuable timber wood. In regions of its best development in the Austrian Alps it attains ages up to 600 years, diameters to 55 inches B.H. and heights over 150 feet. The oldest tree on record (in Tirol, Austria) was 672 years. The tallest tree, in Baden, Germany, 184 feet.

European larch grows on a great variety of sites differing with respect to both climate and soil. Through its different races and clines it is adapted to 2500 meter-(timberline) as well as 150 meter-sites. In its natural range it is most abundant in the inner valleys of the Alps and in other areas which have a continental-type climate. These areas are characterized by many clear days, abundant incoming radiation, lower than average humidity, considerable yearly and daily temperature fluctuation, and free wind movement. Although these areas with a natural abundance of larch receive less precipitation than areas with few larches, this species does best on soils that are constantly moist and have a good water-conducting capacity. A common, although not universal, point of view is that since larch has a high transpiration ratio (water requirement) it thrives best on sites which are well-watered, well-aerated and also have climatic conditions required for rapid transpiration. However, the excellent growth of larch in the moister, cloudier, more even, oceanic-influenced climate of Baden and other areas in western Germany suggests that rapid transpiration is not necessary for larch. It is suggested that the natural abundance of larch in these areas having a continental-type climate may be related more to the great shade intolerance of this species, as it affects competitive ability, than to conditions affecting transpiration.

The European larch prefers deep, well-aerated, moist, sandy-loam to silt-loam soils. It has been found thriving on soils derived from many different kinds of rocks. Soil fertility and soil reaction have not been found significantly related to larch site quality, but the physical soil properties relating to moisture retention and aeration are important. Larch grows satisfactorily on soils with pH values below 4.5 and it tolerates and thrives on natural, highly calcareous soils with pH values up to 7.8 in

all mineral horizons. It is a species sensitive to poor surface and internal drainage and to soil compaction.

In some of the inner valleys of the Alps larch occurs naturally in pure stands. Its more characteristic occurrence, however, is as mixtures, principally spruce-fir-beech-larch and spruce-larch. Larch is also an important component of artificial mixtures in the beech and oak forest zones of western and central Europe. It is suited for mixtures because it is very fast growing in youth, attains great heights and can be maintained as a head-dominant on good sites. It is very intolerant and its open crown transmits much light and does not injure the more tolerant stand members. It is long-lived and can be managed, in contrast to spruce, on rotations as long as required by its associates. It is deep rooted and windfirm. It generally does not form raw humus in central Europe and when mixed with tolerant species may improve soil conditions.

Recommended larch mixtures are beech-larch, oak-larch, pine-larch, beech-oak-larch or beech-oak-pine-larch. The most successful mixtures are attainable on the better soils, although timely thinnings to maintain the dominant crown position of the intolerant larch are required.

European larch has been rather widely planted in the northeastern quarter of the U.S. starting about 100 years ago. On suitable sites its growth has been excellent in areas as widely separated as New England and Iowa. It has numerous enemies but, except locally, these do not appear serious enough to preclude its use in future forests. For eastern U.S. it would seem that the low elevation European provenances should prove more adaptable.

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REVIEW by Benson H. Paul

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Various means for controlling wood density are now being sought. The author reports on some relationships of growth, volume, and weight yield of spruce.

Analysis of the wood of 30 spruce trees representing three different stands in Germany is based on specific gravity of the wood throughout the length of the trees and by 10-year groups of growth rings from the center to the circumference in the four cardinal directions at the respective tree heights.

The investigations show that the specific gravity of wood changes with the development and age of a stand along with environmental influences and forest management practices. In even-aged spruce stands, dominant trees as a rule had lower specific gravity than codominant and intermediate trees. Physiologically restricted (suppressed) trees, however, likewise were of low density. Thinnings that promoted the most rapid growth caused formation of lighter wood than in the case of more moderate thinnings and slower growth. The influence of site and location, except elevation, may be obscured by the management practices. Rapidly-grown spruce stands should produce at least 20 percent more wood volume in order to equal the intrinsic weight of wood from moderately-thinned stands. Other advantages of initial full stocking and later moderate thinnings appeared in the improvement of lumber grades. Care in the regulation of growth when stands are rejuvenated is recommended.

Species Crossability in Spruce in Relation to Distribution and Taxonomy

BY
JONATHAN W. WRIGHT

OUR TREE BREEDING philosophy in the Northeast differs from that found in many other regions. One reason for this difference is that planting now plays a small part in the silviculture of the region. There has been little pressure on the tree breeder to produce improved strains for immediate use. Instead we have been able to take what we call the survey approach; we make a survey of possible methods of obtaining improvements before we embark on detailed studies.

We have done this with spruce. This paper is a report on an attempt to correlate species crossability with geographic distribution, morphology, and phylogeny. It includes a brief discussion on the practical possibilities of species hybridization.

The spruce-improvement program of the Northeastern Forest Experiment Station was begun in 1940 at New Haven, Conn., by Ernst J. Schreiner and his colleagues. This program, interrupted by the war, was resumed in 1948.

There was only limited background information available for planning our spruce-improvement program in 1940. This consisted of the early racial trials with Norway spruce, the accounts of the few known natural hybrids, and the performance records of the many exotic species that can be grown successfully in the Northeast. The first step in our survey approach was to dedermine the species crossability pattern.

The establishment of a correlation between species crossability and morphology, geographic range, or phylogeny proved to call for more than mere compilation of available data. There are excellent range maps for Japan, North America, and northern Europe; but new maps had to be prepared for other regions. It was necessary to delve into the systematics of some of the little-known Chinese species, and it was necessary to re-examine the phylogenetic concepts developed by previous workers.

There are still three serious obstacles that prevent a complete understanding of species crossabilities. One is the relative paucity of information on fossil history. Lindquist's (1948) and Hulten's (1937a, 1937b) excellent researches provide information on the post-glacial history of the boreal species but we have little knowledge of their pre-glacial history. There is almost no information on either pre- or post-glacial distribution of other species.

This study was conducted in cooperation with the Morris Arboretum of the University of Pennsylvania, Philadelphia, Pa., which provided many of the trees used in the research, as well as office and nursery space. Thanks are also due to other arboreta, mentioned in the text, for the use of their trees. Dr. H. L. Li was very helpful in translating some of the Chinese and Japanese references cited.

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The second obstacle is the unsatisfactory taxonomic status of many of the Asiatic species. This is not a reflection on the skill of the taxonomists. It is due to the fact that these species grow in inaccessible regions and are therefore represented by meager collections. Although the author believes that certain name changes would be desirable, he has not suggested them in this paper because the really difficult cases can be solved only by extensive field study.

The third obstacle to a complete understanding of species crossabilities is the fact that up to now controlled pollinations have been made on too few specimens and in too few localities.

Material and Methods

Most of the parent trees used are located in the Morris Arboretum of the University of Pennsylvania; in the Westtown School Arboretum, Westtown, Pa.; or on the campus of Haverford College, Haverford, Pa. A few Norway and white spruces located on private grounds were also used, and pollen of some species was obtained from the Arnold Arboretum of Harvard University, Jamaica Plain, Mass., and from the Institute of Forest Genetics of the California Forest and Range Experiment Station, Placerville, Calif. Identifications of all parents have been checked by the author and when possible by competent authorities such as Alfred Rehder. Common names of American and foreign species follow Little's Check List (1953b) and Rehder (1940) respectively.

Pollen was collected by bringing in nearly open male catkins and letting them shed on paper in light at room temperatures. Shed pollen was collected once daily. In most cases 1 to 3 days were required for pollen extraction. Catkins that were collected too early to shed in 3 days usually did not shed at all. The pollen was stored at 25 percent relative humidity in a refrigerator.

Since several tests of year-old pollen had proved successful, it was used if fresh pollen was unavailable; in table 1 no distinction is made except for intraspecific crosses. Most of the crosses on early blooming *Picea asperata* and *P. glauca* female involved year-old pollen, whereas most crosses on the late-blooming *P. abies* and *P. omorika* females involved fresh pollen. Frequently pollens of several trees of the same species were mixed when trying a cross for the first time.

There is very little spruce pollen in the air near Philadelphia because almost all the species are uncommon there. Hence it was unnecessary to bag the flowers before pollination. Except in 1948 (when the flowers were bagged) the pollination procedure consisted of merely dipping unbagged flowers into a pollen vial and labelling the branches. This technique allowed one man to pollinate 10 to 20 times more flowers in a season than he could have if he had bagged all flowers. This procedure was quite satisfactory for all species except Norway spruce. This species was a heavy pollinator in 1953 and the results for many Norway spruces had to be discarded because of the high seed sets to open pollination.

The control-pollinated cones were collected from 2 days to a week before natural cone opening was due to start. The cones were spread out in warm rooms to open. The seed was collected by vigorous shaking of the opened cones and by dissection of cones that failed to open. After de-winging, the seed was placed in 95 percent alcohol for a minute or two. Floating seeds were discarded as empty; sinking seeds were kept as full. Whenever numbers of seeds permitted, cutting tests were made to determine whether alcohol flotation was giving complete separation of empty and full seeds. The submersion in alcohol had no apparent effect on seed viability.

Within the limits of the available material, at least two tree $\times$ tree combinations in each of two different years were devoted to each cross. Apparently successful crosses were repeated as often as possible. Success

TABLE 1. Summary of artificial crossing work, 1948–1953.

Female parent	Male parent																	Intraspecific, year-old pollen	Intraspecific, fresh pollen
	Wind	Self	glauca (7-5)[1]	mariana (1-1)	rubens (8-1)	engelmannii (2-2)	jezoensis var. hondoensis (1-2)	maximowiczii (1-1)	koyamai (1-2)	asperata (6-5)	retroflexa (1-2)	balfouriana (2-2)	montigena (2-3)	wilsonii (1-2)	abies (6-5)	orientalis (4-2)	omorika (6-2)		
glauca (21-5)[1]	2136 0.2	47 1.2		13 5.0	167 0.3	210 1.3	1637 5.3	262 0.2	99 2.6	415 0.3	79 0.3	298 0.1	43 0.1	185 0.1	140 0.1	108 0.3	90 0.2	116 17	720 11
mariana (1-4)	76 0		60 0					16 0		35 0	14 0	59 0	17 0		92 0				
engelmannii (2-1)	23 0.2	2 0	8 10					3 0.1		7 0.5	3 0.3		2 0		9 0.5	6 0.7			4 1.2
jezoensis var. hondoensis (1-1)			4 21								3 0.7		4 0.2			2 1.0			
maximowiczii (1-1)	19 0		19 0							5 0			5 0		18 0				
asperata (6-3)	983 3.3	35 1.8	1 1.0						2 6.0		2 6.5		21 3.3		175 16			3 12	1 172
retroflexa (1-1)	3 3.0		1 3.0							3 4.0					2 2.0				
montigena (2-3)	128 1.3	5 0	32 1.4					32 0.5	2 35	71 18	5 5.2				124 5.3	2 0	1 0	21 0.2	14 5.6
abies (19-6)	318 3.7	3 0.3	3 0					2 0.5	22 17	280 8.3	1 0		82 10			20 8.0		8 10	31 44
omorika (8-4)	1036 4.9	4 5.0	32 2.2			15 2.1			152 14	14 1.4		85 0.6	27 3.6	56 0.3	24 3.6	426 9.2			58 5.0

[1] Figures in parentheses after the species name indicate the number of trees used as parents and the number of years the species (but not necessarily the individual tree) was used as a parent. Few of the interspecific crosses were made on all parent trees and in all years.

Successful or probably successful crosses

1036 / 4.9 — Number of cones harvested. Number of filled seeds per cone

or failure of a cross in a given year was judged by comparative sets of filled seeds following wind pollination and hand pollination on the same female parent. Whenever necessary the significance of the increased seed sets was determined by Chi-square tests.

As rapidly as possible the authenticity of all supposed hybrids will be checked by study of the seedlings resulting from the controlled pollinations. To date this has been possible for only a few of the combinations.

The progenies resulting from the controlled pollination work are being grown in the nurseries of the Morris Arboretum of the University of Pennsylvania at Philadelphia, of the New York State Conservation Department at Saratoga Springs, and of the New Jersey Department of Natural Resources and Economic Development at Washington Crossing.

Results of Controlled Pollinations

Results of the controlled pollinations are summarized in Table 1. Only the number of cones harvested and the number of good seeds per cone are included because all pollinations gave high sets of cones and empty seeds (Wright, 1953).

In *P. omorika*, *P. abies*, and *P. glauca*, the open-pollinated seed probably resulted from pollination by neighboring trees of the same species. In the other species, specimens of which were partially or completely isolated, much of the open-pollinated seed probably resulted from pollination by another species.

The few self-pollinations tried indicate a low degree of self-incompatibility. More extensive experiments with *P. abies* (Andersson, 1947) showed a high degree of self-compatibility in many trees of that species.

Properly stored year-old pollen was just about as effective as fresh pollen. Intraspecific seed sets were even higher with year-old pollen than with fresh pollen on *P. glauca*, and all successful interspecific crosses on *P. glauca* and *P. asperata* females involved year-old pollen.

With the exception of *P. omorika* × *orientalis*, all crosses gave essentially similar results when repeated with different trees and in different years. In that cross, one pollen of *P. orientalis* was ineffective on three different females whereas pollen from another tree was effective on three other females the same year.

Seventeen interspecific crosses were tried reciprocally (Table 1). Of these, nine failed and five succeeded in both directions, and three crosses gave reciprocally different results, as shown in the following tabulation.

Female and male parents	Crosses made: Parent combinations	Crosses made: Flowers pollinated	Crosses successful: Parent combinations	Crosses successful: Cones matured
asperata × retroflexa	1	2	1	2
retroflexa × asperata	1	3	0	0
glauca × asperata	12	415	2	15
asperata × glauca	1	1	0	0
glauca × mariana	2	13	1	7
mariana × glauca	6	60	0	0

At present little importance can be attached to these reciprocal differences because of the small scale of the work.

The putative hybridity of the following crosses has been established by growth performance in the Philadelphia experimental nursery as well as by seed-set data: *P. glauca* × *engelmannii*, *P. glauca* × *jezoensis*, *P. glauca* × *koyamai*, *P. engelmannii* × *glauca*, *P. omorika* × *orientalis*, *P. asperata* × *abies*, *P. abies* × *koyami*, *P. abies* × *orientalis*, and *P. abies* × *asperata*. In each case hybridity was established by study of the morphological and growth characters of hybrid and non-hybrid progeny from the same female parent. Judging by the results in other genera (for example, the white pines) it may take 5 or more years of such observation to establish hybridity of some other lots.

A summary of all reported species hybrids in spruce is given in Table 2. The parents are arranged by geographic range to accentuate the relationship between distribution and crossability (see later). Omitted from the table are the putative natural spruce-hemlock hybrids reported by Van Campo-Duplan and Gaussen (1949) and by Vabre (1954).

Distribution and Taxonomic Status of Individual Species

The range maps (Figs. 1, 2, 3, 4, and 5) were compiled from the following sources:

Europe: Elwes and Henry (1906, 1912), Erdtman (1933), Lindquist (1948), Fukarek (1950).
America: Munns (1938), Halliday and Brown (1943), Martinez (1953).
Japan and Kamtchatka: Wilson (1916), Hulten (1937a), Hayashi (1952).
China and Manchuria: Rehder and Wilson (1914), Tang (1931), Fenzel (1932, 1933), Cheng (1939), Ku and Cheo (1941), Nakai (1941, 1943), Teng (1947a), Bulard (1947).
Formosa: Hayashi (1952).
Siberia: Elwes and Henry (1906, 1912), Komarov (1934).
Central and southern Asia: Elwes and Henry (1906, 1912).

Whenever possible, specific references dealing with a single species or region were used in preference to such general references as Elwes and Henry (1906, 1912) and Schmucker (1942).

The range maps are most accurate and complete for Japan, North America exclusive of Mexico, and Europe. They are rea-

TABLE 2. Summary of reported crosses in the genus Picea.

Female parent	Male parent: glauca	mariana	rubens	engelmannii	purpurea	sitchensis	breweriana	jezoensis var. hondoensis	maximowiczii	koyamai	asperata	retroflexa	halfouriana	montigena	wilsonii	obovata	abies	orientalis	omorika
glauca	H 15,16	U-16 F-3	F 3,16	H 5,16	F 3	F 3		H 11,16	F 16	F-4 H-16	U 16	F 16	F 16	F 16	F 16		F 3 15,16	F 15,16	F 16
mariana	F 2, 3,16		F 2					H* 11	F 16		F 16	F 16	F 16	F 16		F 2	F 3,16		
rubens		H 3,13															F 3		
engelmannii	H 7, 11,16			U 16		H 1,5			F 16		F 16	F 16		F 16			F 16	F 16	
sitchensis	H 6,7, 9,12			H 5	F 2												H 6		H 2
jezoensis var. hondoensis	H 7,11, 14,16	H 11										F 16		F 16				F 16	
glehnii								H 11											
maximowiczii	F 16										F 16			F 16			F 16		
asperata	F 16					F 2				U 16		U 16		H 16		H 2	H 16	F 2	
retroflexa	F 16										F 16		H* 1				F 16		
montigena	F 16								F 16	H 16	H 16	H 16		H 16			H 16	F 16	F 16
abies	F 3, 15,16	H 3	H 3						F 16	H 16	H 16	H 16		H 16		H* 8	H 16	U-15 H-16	
orientalis	F 2,15				F 2											F 2	F 15		
omorika	F-16 H-10	H 10		F 16		H 10	F 2			H 16	F 16		F 16	F 16	F 16	F 2	F 16	H 16	H 16

*Direction of cross unknown.

H—Putative hybrids obtained.

U—Undetermined; possible hybrids.

F—Failure.

Putative hybrids obtained.

Authorities

1. Cheng 1939
2. Ekstandh 1943
3. Heimburger 1954 (personal communication, superseding and correcting Johnson and Heimburger 1946)
4. Johnson, A.G. (personal communication)
5. Johnson, L.P.V. 1939
6. Langner 1952
7. Larsen 1948
8. Lindquist 1948
9. Little 1953
10. Oxabjerg 1953
11. Rehder 1940
12. Thaarup 1945
13. Westveld, M. 1954 (personal communication)
14. Yanagisawa 1954
15. Northeastern Forest Experiment Station (unpublished data 1937-41)
16. Author's studies

sonably accurate but probably not complete for China and Mexico. And they are least accurate for Asia outside of China.

The Chinese and Manchurian species have been grouped into complexes. Only the complexes were mapped separately, although range data for the component "species" are included in the text. These component "species" are here maintained as such although the author feels that further study will reduce some of them to synonymy and will show others to be geograhic varieties or products of introgression.

P. GLAUCA (Moench) Voss.— WHITE SPRUCE

White spruce ranges across boreal America from coastal Alaska to the northern parts of the Great Lake States, Newfoundland, and New England, and southward along the east slopes of the coastal and Rocky Mountain ranges of western Canada. There is an isolated population (*P. glauca* var. *densata* Bailey) in the Black Hills of South Dakota. Much of the Alaskan material may be referable to *P. glauca* var. *porsildii* Raup (Raup, 1947). Over most of its range it is common, often form-

SPECIES	BUDS	LEAVES	RESIN CANALS	CONE SCALES	COMES	FEMALE FLOWERS	MALE FLOWERS	SEED	GROWTH
	1 Conic, Ovoid, Subglobose 2 Acute, Obtuse 3 Resinous 4 Color 5 Length 6 Terminal bud scales Keeled, Subulate 7 Needles around terminal bud 8 Scales Appressed, Loose 9 Scale Acute, Obtuse, Round 10 Scales Entire, Scarious, Lacinate	11 Length 12 Tall, 4-sided, Compressed, Flat 13 Acute, Obtuse, Sharp 14 Stiff, Flexible 15 Green, Blue 16 Pectinate, Radial, Forward, Upward 17 Curved, Straight 18 Stomata rows above 19 Stomata rows below 20 Keeled above, Below, Two sides 21 Resin canals, number 22 Resin canals Peripheral, Medial 23 Skunk odor	24 Diameter 25 Color 26 Pubescent, Glabrous 27 Lustrous 28 Pulvinal Swollen 29 Sterigmata Short, Long	30 Rhombic, Circular, Obovate 31 Apex Entire, Denticulate, Erose 32 Apex Reflexed 33 Apex Undulate	34 Color, Immature 35 Color, mature 36 Length 37 Retained 1 year, 2+ years	38 Length 39 Color 40 Bracts Entire, Denticulate, Laciniate 41 Bracts Exposed 42 Scales Reflexed	43 Length 44 Color	45 Seed Length 46 Seed + wing Length 47 Color	48 Max. Ht., feet 49 Alt., South, 1,000 feet 50 Alt., North, 1,000 feet 51 Epicormic branches on bole	
1 glauca	OO-OI--LOS	S4AIIMRISS	ILG---I	CN---	IRQD-R	VST	SR		100	2-5	0-	-
2 mariana	OA-SS-AAS	VS4SFIMRISS	VKAIIS	CD---	VGRD-R	VBS	VR		100	2-3	0-2	-
3 rubens	OA-SS-AAS	S4OSGIMRISS	VKAIIS	CD---	VPSB	VBS	VR		110	4-5	0-2	-
4 engelmannii	OO-SI-IOE	I4APBPSSS	IKAIIL	RE--U	VRD-R	VSB1	VR		150	9-11	3-5	-
5 pungens	OA-OI-IAS	L4SSBRCSS	LKCIIL	RE--U	GM--R	VPI	SY		150	6-10		-
6 chihuahuana	OA--AAL	I4SSGRCLL2P	KGI--L	ON---	ME--	S	L		100	8		-
7 aitchensis	OORHS---IOS	I4SPGRSIVT2M	SLG---L	REE--U	YGMI--	I	LR		200	0-2	0-1	M
8 breweriana	OA-SI--IAE	I4OSGRSSIOT2M	SCP--IEL	ON----	GPOEI-	GL--	SRP		200	5-7	4-5	
9 jeffreyi	OORHS---IAE	I4APGPIOIT2M	IKGLIEL	REE--U	GMII--	IRPD-R	LRP		120	4-8	0	
10 glehnii	OORHS---IAE	V4OSGPCIS	I881I--L	CN---	PBI--	VRPD-R	VR		150	6-10		
11 bicolor	OAIHI--IARE	S4AIGRIEV	SHILSII	RDR--	RPTE--				115	2-7		M
12 maximowiczii	OAR-S---ARE	V4SSGRSII2P	IKG--IL	ON----	YGMIS--	D--			150	4-7		
13 polita	OO--I---ARE	I4SSGRSEE2P	LKGL--L	OD----	YGMIL--				150	5-6		M
14 morrisonicola	OO-RHS---AOS	S4AIGRSIIOT2M	SLG--SL	OD----	RPBII--				130	10-13		
15 koyamai	OARHI---AOS	V4OSGPCIS	I881I--L	CD---	PBI--	IRPD-R	LRP		130	10-13		
16 asperata	CARDKNIOS	S4OSIRIIII	LHIIIIL	CD---	YGML--	I--R		SSB	130	5-11		
17 retroflexa	CARDKNIOS	I4SSIGPCSIOT	VHIIISL	RD---	OQL---	I R			130	10-13		
18 likiangensis	CAMDKNIOE	SCAIGPSIOT	IKAIISL	RD--U	YGMIL--		I		130	10-13		
19 balfouriana	CAMDKNIRE	S4OSGPSIOT	SCLL-L	RD---	RPBII--			SS	130	10-13		
20 montigena	CARCKNIRE	S4OSBRCIS	FCPL-L	RE---	PMI--	-R	IP	SSB	65	9-11		
21 wilsonii	SOO-RS--AOE	ICAPGPSLS2P	SGG---S	OD---	GMI1	VRP	-R	E	SSB1	150	8-10	
22 purpurea	OOO-OSK-ARE	VSCIOPGPC1OVT	SGGP---S	REE---	PBS--					130	8-12	
23 brachytyla	OO-RI--AOS	SIPIOPGP-B4M	VKG---S	ON----	PMI--		-R	E	VSB	90		
24 complanata	OA-RI--IARE	SIPIS GRSIOT4M	ICG---SL	ON----	GBL--				VSB	130	4-11	
25 spinulosa	OO-RL--NOS	ECSSGRSIOT2M	ILG---L	CD--U	GPML--				SSB	220+	9-10	
26 obovata	CA-OIKNAOE	SIOPGRISV	ILIII--I	ON---	POOI--	IR	-R		VSD	160		0-
27 schrenkiana	SOO-OLKNAAS	E4SSGPIII	SLG---I	ON--U	RL--				ISD	115	8-10	4-8
28 saitoiana	OOORLKIARE	E4SSGRSVV	SLGL--I	CN---	GOSS--			IV	LLD	215	7-11	
29 abies	CA-RLKILAS	S4AIGRSSS2P	LHIII--I	RD---	GOOE+--	L	RD-R	IR	IID	160	3-6	0-3
30 orientalis	OA-OSKNARE	V4OSGRSII	IKPL--L	ON---	PMI--	RG	--	VR	ISB	180	3-7	-
31 omorika	OA-RSSNAAE	ILEQEGPISOT	IKP---L	CD--U	PBS2+	SR	-R	SR	VVB	184	3-5	-

[1] Certain Chinese species of doubtful taxonomic status are omitted.

TABLE 3. Morphological characters of the spruce species.[1] (Symbols are explained in text.)

ing pure stands. It is usually an aggressive pioneer species.

According to Raup (1946) there were no extensive forests in central or southern Alberta and Saskatchewan in late Wisconsin times, and the forests did not appear in the southern part of the Mackenzie Basin until the ice was gone from Great Slave Lake, possibly 7,000 to 9,000 years ago. Evidently the species survived the Pleistocene in such glacial refuges as the Yukon Basin in Alaska, the Black Hills, Gaspé Peninsula, and parts of Prince Edward Island, Labrador, and Newfoundland. There is one record of its Pleistocene occurrence in Louisiana (Brown, 1938).

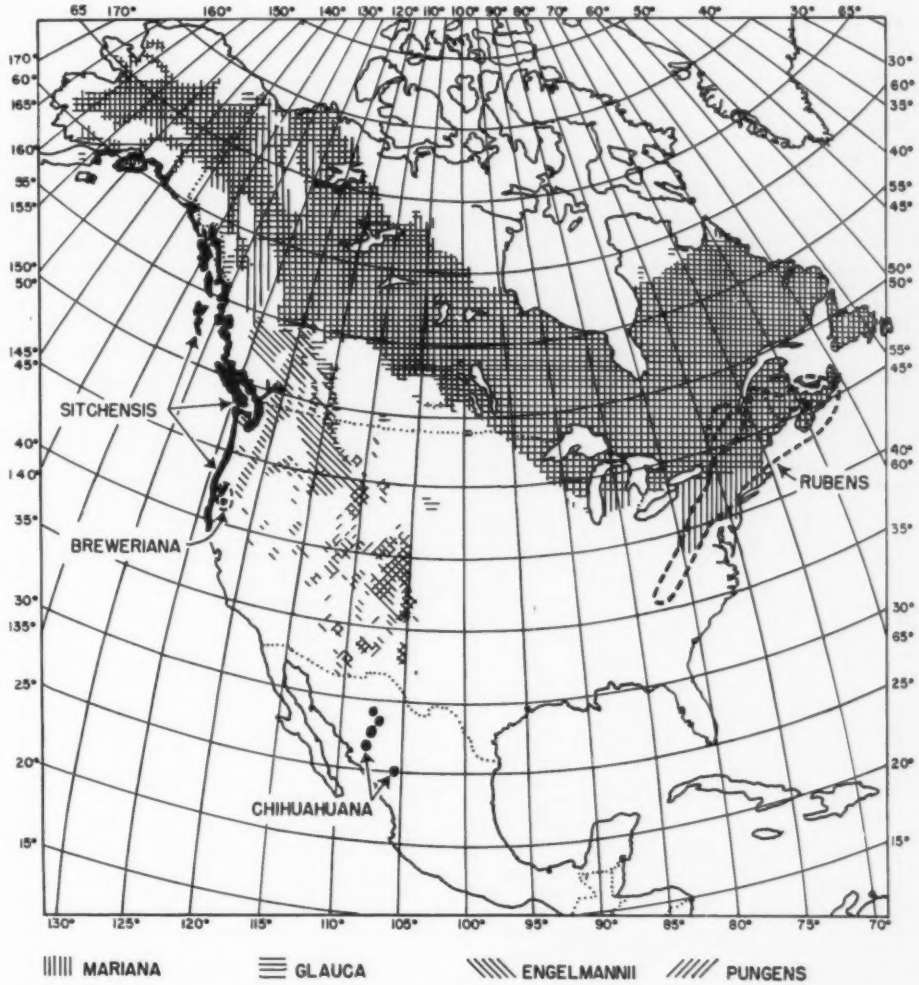

FIGURE 1. Distribution of the North American species of Picea. *Most of the species have continuous distribution as shown by the map.*

White spruce is morphologically distinct from red and black spruce and does not cross naturally to any extent (if at all) with either[1] even though it is sympatric with both. A few seeds were obtained from artificial crosses with black spruce.

White spruce has a slight range overlap with Sitka spruce on the Kenai Peninsula and nearby Chugach Mountains in Alaska. There the two species cross, producing *P.* × *lutzii* Little (Little 1953a). As Sitka spruce probably survived the Pleistocene only in the southern part of its present range (Hulten, 1937b) the present range overlap and hybridizations are probably recent phenomena. The presence of several generations of natural hybrids between these species in Denmark (Thaarup, 1945) indicates that there are few or no genetic barriers to crossability between the species.

The excellent crossability of *P. glauca* with *P. jezoensis* suggests that the Alaska-Kamtchatka range gap was opened in relatively recent times.

Along the east slope of the Canadian Rocky Mountains is an extensive zone of contact between white and Engelmann spruces. The white spruce population in and near this zone of contact was treated as *P. glauca* var. *albertiana* (S. Brown) Sarg. by Sargent (1922), Elwes and Henry (1912), and Rehder (1940). However, Elwes and Henry mentioned the possibility that the variety was of hybrid origin. Little (1953a) mentioned the presence of natural hybrids in the zone of overlap. As explained below, this population is probably a yet unstabilized introgression product and should not be given varietal status.

A small supplementary taxonomic study was made to determine the extent of this hybridization. The following material was used: white spruce from British Columbia and Alberta from the Arnold Arboretum and Gray Herbarium of Harvard University, and "typical" white and Engelmann spruces from well outside the zone of overlap from the herbarium of the Morris Arboretum of the University of Pennsylvania. Each specimen was scored for needle stoutness, presence of bloom on the branchlets, and 13 other diagnostic characters listed in Table 3. From the results of the scoring, indices were calculated:

Engelmann character index = (number of trees × characters deviating from "typical" white spruce)/ (total number of trees × characters)

For various reasons these indices can be regarded as only relative measures of the degree to which Engelmann spruce germ plasm has infiltrated white spruce. The indices are presented in the following tabulation.

Locality	Trees scored *Number*	Engelmann character index
White spruce far distant from zone of contact		
Eastern U.S.	7	0.06
S. Dakota, Saskatchewan	3	.13
White spruce near zone of contact		
Jasper National Park, Alberta, and adjacent British Columbia, 53° N., 119° W.	21	.34
Banff, Alberta, and adjacent British Columbia, 51° N., 116° W.	12	.52
White spruce 100 or more miles away from zone of contact		
Wood Buffalo Park, near Lake Athabasca, Alberta, 59° N., 109-113° W.	8	.29
Peace River Valley, Alberta and British Columbia, 56-58° N., 117-124° W.	8	.31
"Typical" Engelmann spruce		
Western U.S.	6	.94

The characteristics of the "typical" white and Engelmann spruces are based on few specimens, but they agree with published descriptions based on large numbers of specimens.

Although the Jasper Park, Lake Athabasca, and Peace River collections have about the same hybridity indices, they do not possess the same characters and should not be considered as a single geographic variety. For the present it is best to describe aberrant populations in this region in appropriate English terms.

[1]Personal communications from C. Heimburger and M. Westveld.

P. MARIANA (Mill.) B. S. P.—BLACK SPRUCE

Black spruce is the widest ranging of the American species. It covers almost the entire range of white spruce from Alaska to Newfoundland except that it does not go far south in the Rocky Mountains and does not get into the Black Hills. In addition it occurs in unglaciated areas in the northern Appalachians. Presumably it spent the Pleistocene in company with both white and red spruce. It is typically a swamp tree and for that reason it is usually separated ecologically from the other species although nearly always there is an opportunity for crossing to occur.

Natural hybrids with red spruce do occur (Heimburger, 1939). No natural hybrids with white spruce have been reported, although probable artificial hybrids were produced from one tree × tree combination.

The range of black spruce approaches those of Engelmann and Sitka spruces but apparently does not overlap them as does the range of white spruce.

P. RUBENS Sarg.—RED SPRUCE

Red spruce is a moderately wide-ranging species, growing from the southern Appalachians to the Maritime provinces of eastern Canada. It stops short of the large unglaciated areas of the Gaspé Peninsula and Newfoundland; it probably spread northward into glaciated areas occupied by white spruce since the Pleistocene. The occurrence of both black and red spruce in unglaciated parts of Pennsylvania and West Virginia indicates that these species have been sympatric for a much longer time. It is usually separated ecologically from black spruce but occurs on the same sites as white spruce.

Westveld[2] and Heimburger[2] have recognized no red × white spruce hybrids in long years of experience with the spruce-fir forest.

Westveld[2] and Heimburger (1939) found probable red (female) × black spruce hybrids near a bog at Gale River, New Hampshire. The hybrids constituted a small percentage of the reproduction and occurred on the upland portion of the narrow ecotone between typical red and black spruce sites. The occurrence of hybrids near this bog is probably related to the fact that a previous fire had reduced the red spruce stand, improving the chances for the production of hybrid seed and for survival of hybrids. Westveld found red × black spruce hybrids under similar circumstances in eastern Maine.

In a later section of this paper it is brought out that most southern species have small and shrinking ranges, whereas most northern species have larger, expanding ranges. The following facts indicate that this generalization holds for the red spruce (southern) and white spruce (northern).

In northern New England three different trends affect the range relationships of red and white spruce (Westveld).[2] (1) Red spruce has nearly disappeared from over a million acres of spruce-hardwood forest as a result of repeated logging of the spruce to a small diameter limit. (2) In many areas white spruce is increasing its range as a result of its ability to invade abandoned farmland. (3) In mixed spruce stands red spruce tends to replace white spruce because of greater tolerance. The net effect of all three trends is a shrinkage of the red spruce range and an expansion of the white spruce range.

In the southern Appalachians Korstian (1937) notes that:

> . . . the usefulness of this (red) spruce forest for saw timber and pulpwood has resulted in large-scale exploitation, followed generally by fire, and leading to virtual destruction of type. . . . On deep, well drained soils the proportion of spruce and fir reproduction that comes in after heavy logging is reduced through the encroachment of aggressive hardwoods. . . . If the southern spruce forest is to be perpetuated it must be managed very judiciously.

[2]Personal communication.

Since 1939 the New York State nursery at Lowville, N. Y., has attempted to grow red spruce five different times. All sowings were nearly complete failures, despite the facts that Lowville is only a few miles away from native red spruce stands and that Norway and white spruces are successfully grown in the nursery. Most of the red spruce mortality occurred after the first summer. The exact cause is unknown.

P. ENGELMANNII Parry— ENGELMANN SPRUCE

This is a widespread and important timber tree of the interior (and to a lesser extent the coastal) mountains of the western United States and Canada. It is usually found associated with sub-alpine fir or in pure stands. It is less tolerant than the subalpine fir although more tolerant than most of its other associates.

Engelmann spruce has a possible range overlap with Sitka spruce, and extensive range overlaps with blue and white spruces. A. G. Johnson[3] reports the presence of putative natural hybrids with blue spruce, and there is introgression with white spruce.

P. PUNGENS Engelm.— BLUE SPRUCE

Blue spruce is a relatively uncommon, yet widely distributed, tree of the southern Rocky Mountains. A few putative hybrids with Engelmann spruce have been reported by Johnson.[3]

P. CHIHUAHUANA Martinez

Judging by the fact that it was only described in 1942, this is a rare species within its limited area distribution. Although Martinez commented that it was similar to blue spruce, it seems much more closely related to some Japanese and Chinese species.

P. SITCHENSIS (Bong.) Carr.— SITKA SPRUCE

Sitka spruce ranges from Kodiak Island in the north to northern California. It is unique among the spruces in being a lowland tree even in the southern portion of its range, and is limited to coastal forests below 3,000 feet (much lower in the north). No geographic varieties have been described but north European foresters recognize geographic ecotypes; they generally prefer seed from the Queen Charlotte Islands, Canada. Its present range north of the United States has probably been occupied since the Pleistocene; during the Pleistocene it was probably restricted to the southern portion of its present range (Hulten, 1937b). It usually comes in early in forest succession and is a minor component of the climax forest. Because of its northern distribution in Alaska, and because of its close taxonomic and genetic relationships with other northern species, Sitka spruce is best regarded as a northern species in spite of the fact that it grows at low altitudes in temperate regions.

There is a slight range overlap and natural crossing with white spruce in Alaska. It approaches but probably does not overalp the range of Englemann spruce; however, hybrids between the two occur in Denmark. In slightly warmer pre-Pleistocene times Sitka spruce probably grew on the Aleutians and was linked to *P. jezoensis*, to which it is similar taxonomically.

P. BREWERIANA S. Wats.— BREWER SPRUCE

This species has the smallest range of any American species, being confined to a few mountains in southern Oregon and northern California, where it occurs in mixed stands at altitudes of 4,000 to 7,500 feet. Natural regeneration is scarce and nursery stock is very difficult to raise (Elwes and Henry, 1906). Brewer spruce is most similar to some of the south Chinese species. It probably is an offshoot of an earlier migration than the one that gave rise to the other spruces of northwest America.

[3]Personal communication.

P. JEZOENSIS (Sieb. and Zucc.) Carr.—YEDDO SPRUCE

This has the widest range of any of the eastern Asiatic spruces. On the mainland it reaches its northern limit near Ayan, Siberia and in the nearby Stanovoi Mountains, thence stretching south on hills and in swamps near the coast to Amurland and northern Korea and inland on the Burreya Mountains (low shrub at timberline) and the mountains of all provinces of Manchuria to its western limit in the Weichang, Jehol, China. It also occurs in central Kamtchatka, on the three southernmost Kurile Islands, on Hokkaido, and on Honshu, where it is the high-altitude spruce (1,200 to 2,650 m.). Throughout most of its range it is a common tree. (Elwes and Henry, 1906; Wilson, 1916; Komarov, 1934; Hulten, 1937a).

In Kamtchatka and the Kuriles this is the only spruce present. It has a slight range overlap with Siberian spruce along the sea of Okhotsk. In Korea and Manchuria it is sympatric with *P. koyamai* and possibly Siberian spruce. On Hokkaido it grows with *P. glehnii*. On Honshu it is sympatric with all the other Japanese species.

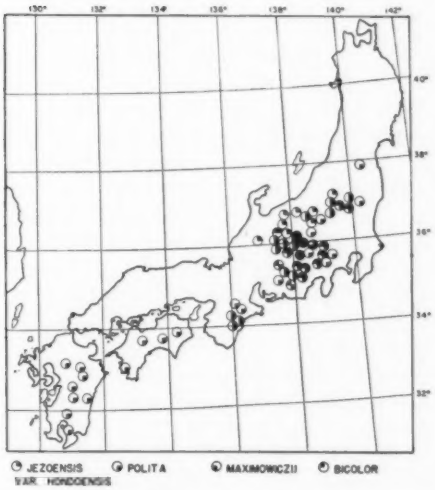

FIGURE 2. Distribution of species of Picea *on the three southern Japanese islands. The species have more discontinuous ranges than shown on the map. The Japanese portion of the range of* P. koyamai *is a small area on Mt. Yatsugatake, 138° 30′ E., 36° N.*

Here it seems best to follow Rehder (1940) and Hayashi (1952) in recognizing only one geographically variable species with the variety *P. jezoensis* var. *hondoensis* (Mayr.) Rehder on Honshu. Elwes and Henry (1906) maintained the Honshu portion of the population as specifically distinct (*P. hondoensis* Mayr.) from the rest of the population (*P. ajanensis* Fisch. = *P. jezoensis*). Gaussen and Lacassagne (1930) presented unconvincing arguments for recognizing three sympatric species in Kamtchatka (*P. jezoensis*, *P. ajanensis*, and *P. kamtchatkensis* Lacassagne), basing a new species on portions of six previously collected specimens. Still more recently Vasiljev (1950) recognized five species (*P. jezoensis*, *P. hondoensis*, *P. microsperma* (Lindl.) Carr., *P. komarovii* Vasiljev, and *P. ajanensis*). These species were all regarded by their authors as closely related to each other.

This species is morphologically distinct from and probably does not cross to any extent with its sympatric species. The one such natural hybrid reported (*P. glehnii* × *jezoensis*; Rehder, 1939) occurred in cultivation.

P. jezoensis is the most probable connecting link between the Old World and the western American species. It is similar taxonomically to Sitka and Englemann spruces and crosses easily with white spruce. In all probability its range overlapped that of one of the American species (Sitka?) in the not-too-distant past. The 1,500-mile gap between the present ranges of *P. jezoensis* and the American spruces contains the Aleutian islands on which planted Sitka spruce grows. Japan-Aleutians-Alaska, Japan-Kamtchatka-Aleutians, and Alaska-Aleutians distributions are common in living groups and nearly all the present Aleutian flora is derived from Japan-Kamtchatka or Alaska (Hulten, 1937a, 1937b.)

P. GLEHNII (Fr. Schmidt) Masters.—SAKHALIN SPRUCE

This has the smallest range of any of the northern spruces, being found only in southern Sakhalin and the mountains of Hokkaido. Its range is entirely within that of *P. jezoensis*, with which it frequently occurs in mixed stands. It is sympatric with no other spruce. In the north it occurs commonly in pure swamp stands but it is more frequent in mixed upland stands. It is most similar to the Formosan and certain south Chinese species.

P. BICOLOR (Maxim.) Mayr.—ALCOCK SPRUCE

This is a tree of limited distribution at elevations of 700 to 2,200 m. in central Honshu. It is moderately tolerant, usually occurs in mixed stands, and associates at least slightly with all the other Honshu spruces. Three varieties (*P. bicolor* var. *bicolor*, *P. bicolor* var. *acicularis* Shirasawa and Koyama, and *P. bicolor* var. *reflexa* Shirasawa and Koyama), differing in pubescence and cone-scale denticulation but without geographic significance, are recognized by Rehder (1940) and Hayashi (1952).

P. MAXIMOWICZII Reg.

This species was discovered on Mt. Fujiyama but is now known only to the west, having about a 1° range of latitude in or near the Yatsugataka Mountains at elevations of 1,100 to 2,000 m. It is a moderately tolerant mesophytic tree growing in mixed conifer stands. Some natural regeneration takes place. It is frequently associated with the other Honshu spruces.

P. POLITA (Sieb. and Zucc.) Carr.—TIGERTAIL SPRUCE

This species has the widest range of any of the strictly Japanese species, occurring on the southern islands of Shikoku and Kyushu as well as Honshu. It has an elevational range of 400 to 1,850 m. Although it occurs in company with all the other Honshu species, it generally occupies lower elevations than any of them. It is very tolerant and is characteristic of mixed temperate stands.

P. MORRISONICOLA Hayata

This species is endemic on Mt. Morrison, Formosa, where it usually occurs in mixed, inaccessible stands. Morphologically it is most similar to some of the south Chinese species.

P. KOYAMAI Shirasawa

This species was originally discovered (Shirasawa and Koyama, 1913) on the Yatsugatake Mountains in Japan, where there was a grove of about 100 trees. It is now known from two localities in Japan, both within a few miles of each other. This population has always been regarded as distinct from other Japanese species and has retained its original name.

Early in the present century Korea and Manchuria were little known botanically, and spruces collected there were referred to *P. obovata* (Komarov, 1902; Elwes and Henry, 1912; Fenzel, 1932, 1933), or *P. schrenkiana* (Rehder and Wilson, 1914), although Wilson (1916) considered it probable that all might belong to the newly described and relatively unknown *P. koyamai*. In 1919 Nakai described this mainland population as a new species, *P. koraiensis* Nakai, under which name it is treated by Komarov (1934). Modern Japanese foresters[4] consider *P. koraiensis* synonymous with *P. koyamai*. More recently three new species have been described from one locality (Mozan, Korea) in which *P. koraiensis* also grows: *P. pungsanensis* Uyeki, *P. intercedens* Nakai, and *P. tonaiensis* Nakai (Nakai, 1941). The figures and descriptions indicate that these species (each based on only one or two specimens) differ from each other slightly in branchlet and cone color, pubescence, cone-scale shape, and cone and needle length.

The present range of *P. koyamai* may be

[4]Inokuma; personal communication.

described as very limited in Honshu, extensive in the mountains of north Korea (1,000 to 1,500 m. elevation) and extensive in the mountains of Manchuria. In Japan it is sympatric with four other Japanese species with which natural hybrids have not been reported and artificial hybrids have not been attempted. Over most of its range on the mainland it is sympatric with *P. jezoensis* although probably ecologically separated from that species (Fenzel, 1933). In nothern Manchuria or southern Siberia it probably overlaps the range of *P. obovata*. To the south it is now separated from the nearest Chinese species (*P. asperata* and *P. wilsonii*) by about 150 miles, the distance between the Weichang in Jehol and the Wu-tai-shan. However, it was probably connected with the Chinese species during Pleistocene times, since Ma (1947) concludes from the mid-Pleistocene Siobara flora that the vegetational zones were then about 1,000 m. lower than at present.

Four lines of evidence indicate that *P. koyamai* may be considered as one of the most primitive and generalized species in the genus. (1) *P. koyamai* pollen induced the set of full seeds on all five species on which it was used in the present experiments. (2) It is very generalized in taxonomic characters, having few characters not shared by five or more other species, and being extreme only in branchlet color. (3) Its restricted disjunct range in Japan and Korea is rare in high-altitude conifers and is typical of an ancient species. (4) The edge of the Pacific Basin is considered by Li (1953) to be the center of distribution for nearly all conifer genera; and *P. koyamai* occurs on the edge of the Pacific Basin.

P. ASPERATA COMPLEX

This complex includes *P. asperata* Masters, *P. asperata* var. *notabilis* Rehder and Wilson, *P. asperata* var. *ponderosa* Rehder and Wilson, *P. aurantiaca* Masters, *P. gemmata* Rehder and Wilson, *P. heterolepis* Rehder and Wilson, *P. meyeri* Rehder and Wilson, and *P. retroflexa* Masters.

Rehder and Wilson (1914) maintained the species or varieties given above. Later Rehder (1940) omitted *P. gemmata*, considered *P. heterolepis* as *P. asperata* var. *heterolepis* (Rehder and Wilson) Cheng, and maintained the others as minor related species. Cheng (*in* Hu, 1934) considered them all as belonging to the same species (*P. asperata*) but later (1939) maintained *P. asperata*, *P. aurantiaca*, *P. heterolepis*, and *P. retroflexa* as separate species, omitting the others. Growth evidence in Philadelphia shows that at least *P. asperata* and *P. retroflexa* are genetically different.

P. asperata itself is the most widespread member of the complex and has priority of naming. It is the principal member of the complex present in Hopei, Chahar, Shensi, Ningsia, Kansu, Tsinghai, and the Minshan of northern Szechuan. Of the others, only *P. meyeri* is reported within this area, from the Wu-tai-shan of Shansi and from near the Tao River, Kansu. In the remainder of Szechuan and in Sikang, *P. asperata* is absent, being replaced by *P. retroflexa* near Lifan, Szechuan (31½° N., 103½° E.) and near Tatsien-lu, Sikang (29½° — 31° N., 101½ — 102° E.); by *P. heterolepis* near Mowhsien, Szechuan (31½° N., 104° E.); by *P. gemmata* northeast of Tatsien-lu and Sunglingkow, Sikang (29½°—31° N., 101—102° E.).

P. asperata itself is sympatric with *P. wilsonii* in Hopei and the Min-shan of northern Szechuan and with *P. purpurea* in the Min-shan. They are partially isolated ecologically, as *P. asperata* occupies the intermediate altitudes between *P. wilsonii* (low) and *P. purpurea* (high); but with over-cutting in historical times *P. asperata* has been replacing the near-climax forests containing the other two species (Teng, 1947a).

The other members of the complex occur in the same localities as do various members of the *P. likiangensis* complex and in turn

these are nearly limited to localities recorded for members of the *P. asperata* complex. All this, plus the facts that these two complexes show morphological interrelationships (Fig. 6) and cross if given the opportunity (Fig. 7), indicates that many of these "species" are the products of recent introgression. This is substantiated by the fact that *P. asperata* seems to have been a recent migrant to the area of species overlap, as even now it seems to be moving southward following over-cutting (Teng, 1947a). With former geographic isolation there would have been little need for the formation of genetic barriers between the two complexes. Cheng (1939) has already

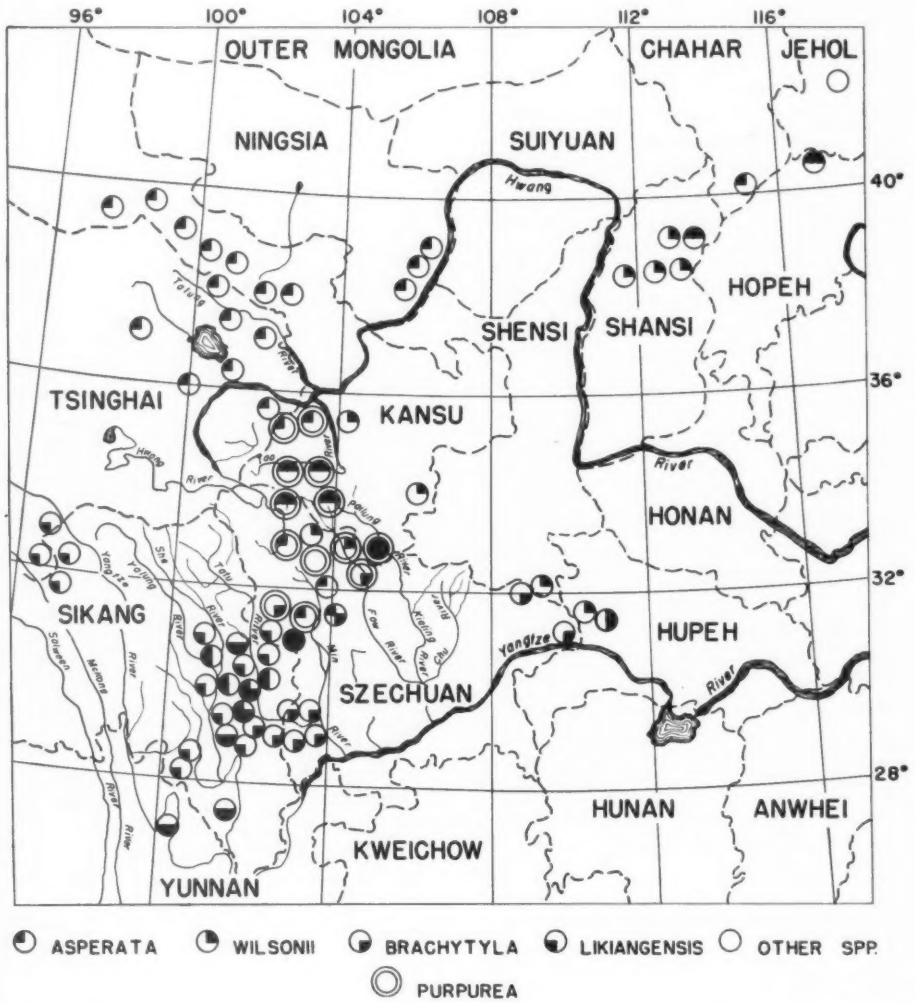

FIGURE 3. Distribution of species of Picea *in China. The species have very discontinuous ranges. See the text for the distribution of the minor "species" included in the various complexes that are mapped here.*

suggested a hybrid origin for *P. sikangensis* (=*P. balfouriana* × *retroflexa*). There is also the alternative hypothesis that the two complexes are now differentiating rather than hybridizing.

P. LIKIANGENSIS COMPLEX

This complex includes *P. balfouriana* Rehder and Wilson, *P. hirtella* Rehder and Wilson, *P. likiangensis* Pritzel, *P. likiangensis* var. *rubescens* Rehder and Wilson, *P. montigena* Masters, *P. sikangensis* Cheng (*P. balfouriana* × *retroflexa*).

Rehder and Wilson (1914) and Cheng (1939) maintained all species then described as such. Cheng (*in* Hu, 1934, and Rehder (1940) considered *P. balfouriana* as a variety (*P. likiangensis* var. *balfouriana* (Rehder and Wilson), Cheng), omitted *P. hirtella*, and considered *P. likiangensis* and *P. montigena* as species. The forester Teng (1947b) treated *P. likiangensis* and *P. balfouriana* as major forest species in the region concerned.

The eastern portion of the complex's range—western Szechuan and eastern Sikang—is occupied by all members of the complex; *P. balfouriana* and *P. likiangensis* are the most common. They rarely occur in the same locality with each other. *P. hirtella* is practically limited to localities in which *P. balfouriana* and a member of the *P. asperata* complex (either *P. retroflexa* or *P. aurantiaca*) are present; *P. montigena* is practically limited to localities in which *P. likiangensis* and a member of the *P. asperata* complex are present. The peripheral portions of the range are occupied by *P. balfouriana* in eastern Sikang and adjacent Tsinghai; *P. likiangensis* in the mountains in the bend of the Yangtze River in northern Yunnan; *P. likiangensis* and *P. montigena* in the most southern locality in Sikang. Members of the complex are allopatric with *P. wilsonii*, *P. purpurea*, *P. asperata*, and *P. brachytyla*, but are commonly sympatric with members of the *P. asperata* complex and are rarely sympatric with members of the *P. brachytyla* complex.

The distribution patterns indicate that *P. balfouriana* and *P. likiangensis* are either well-defined geographic varieties or closely related species, but that the other "species" are products of recent introgression with the *P. asperata* complex.

P. WILSONII Masters

This species is a widespread but relatively uncommon member of low-altitude (1,600 to 3,200 m.) near-climax mixed forests. In parts of Shansi, Shensi, and Hupeh it is the only spruce present. In southern Kansu and northern Szechuan it is sympatric with *P. asperata* and *P. purpurea* and often also with *P. complanata* of the *P. brachytyla* complex. In most of its range it is becoming rarer (Teng, 1947a; Melville, 1950).

Several names applicable to genetically similar material have been used for this species but the confusion has now been cleared up satisfactorily (Melville, 1950). The species seems to be a relatively stable one that is little affected by introgression.

P. PURPUREA Masters

This species is localized in northern Szechuan and Kansu, occurring sympatrically with *P. asperata*, *P. wilsonii*, and occassionally with *P. brachytyla* complex, forming extensive high-altitude forests. It is generally a member of the near-climax forest, and is losing ground to *P. asperata* following overcutting (Teng, 1947a). It has been maintained as a separate species by both taxonomists and foresters. Cheng (*in* Hu, 1934), Cheng (1939), and Rehder (1940) regard it as most closely related to the *P. likiangensis* complex, but it is morphologically most similar to *P. brachytyla* and *P. wilsonii*. Presumably it does not cross with the species with which it occurs sympatrically.

P. BRACHYTYLA COMPLEX

This complex includes *P. ascendens* Patschke (=*P. brachytyla* forma *rhombisquamea* Stapf.), *P. brachytyla* (Franch.) Pritz., *P. complanata* Masters (=*P. brac-*

hytyla var. *complanata* (Masters) Cheng, *P. pachyclada* Patschke, and *P. sargentiana* Rehder and Wilson.

Rehder and Wilson (1914), Cheng (1939), and Bulard (1947) maintained all save *P. pachyclada* as separate related species; Cheng (*in* Hu, 1934) considered them all as part of *P. brachytyla;* Rehder (1940) recognized *P. complanata* and *P. ascendens* as a variety and forma respectively of *P. brachytyla,* considering the other two as synonymous with *P. brachytyla.* In forestry writing Ku and Cheo (1941) recognized only *P. brachytyla,* and Teng (1947b, 1947c, 1948) recognized only *P. brachytyla* and *P. complanata.* Members of the complex inhabit low-altitude (1,600 to 2,500 m.) near-climax mixed forests, and were formerly more abundant than now.

P. brachytyla is geographically separated from the rest of the complex. It occurs east of 108° E. in the Ta Pa Shan of the Shensi-Szechuan border and the mountains of northwestern Hupeh. There it is the only spruce or occurs sympatrically with *P. wilsonii.* The other members of the complex occur in southern Kansu, western Szechuan, and eastern Sikang, where they frequently occur in the same localities with each other. According to Bulard (1947) their ranges are nearly identical. They most frequently occur in the same locality with *P. asperata* and *P. purpurea* and more rarely occur with *P. wilsonii* and members of the *P. likiangensis* complex.

P. SPINULOSA (Griff.) HENRY

Elwes and Henry (1912) report this species from only two localities in Sikkim and Bhutan of the eastern Himalayas and comment that it is rare when found. Allowing for the fact that this region is little explored and that further stations may turn up, we can regard this as one of the southern endemics of extremely limited range. It apparently reaches the largest size of any spruce species, as the largest specimen found measured 220 feet to where a sizable portion of the crown was broken off. The morphological and distributional evidence indicate that its closest relationships are with the southwestern Chinese and Formosan species.

P. OBOVATA Ledeb.— SIBERIAN SPRUCE

Siberian spruce is a wide-ranging species, growing from northern Scandinavia, Finland, and European Russia across Siberia to the Sea of Okhotsk. On the west there is a broad zone of hybridization with Norway spruce, and it is impossible to draw an exact boundary line between the two. On the east it probably overlaps the range of *P. jezoensis* near the coast of the Sea of Okhotsk. Near the Altai Mountains it seems isolated from *P. schrenkiana* (Komarov, 1934) to the south, although on Lindquist's (1948) range map the two species are shown with overlapping ranges. In the older literature (Komarov, 1902; Elwes and Henry, 1912) there are references to Siberian spruce in Manchuria. Now, however, (Komarov, 1934; Rehder, 1940) this Manchurian population is referred to *P. koyamai* (=*P. koraiensis*). Komarov (1934) considered that south of the Amur River Siberian spruce was forced out (replaced geographically?) by *P. koyamai. P. manchurica* Nakai (1943) of northern Manchuria is regarded by its author as a close relative of *P. obovata,* and is probably referable to that species or to *P. koyamai.*

In addition to its main area of distribution there is an isolated outpost of *P. obovata* var. *alpestris* (Bruegger) Henry among the Norway spruce forests of the Swiss Alps

Siberian spruce is regarded by Lindquist (1948) and other taxonomists as a geographic variety of Norway spruce, although many other equally competent taxonomists regard it as a separate species. In most north European forestry literature spruce populations falling within the range of *P. obovata* and probably belonging to that species are referred to simply as *gran,*

Fichte, or spruce, with the inference that Norway spruce is meant.

The crossing data and the extensive Siberian distribution of Siberian spruce indicate that Siberian spruce is the intermediate between Norway spruce and the north Chinese spruces. On the other hand, the morphological data and the Ural range of Siberian spruce indicate that it is the intermediate between Norway spruce and *P. orientalis*.

P. SCHRENKIANA Fisch and Meyer

This species is confined to the Ala Tau and Thian Shan mountains of Turkestan in central Asia. It is relatively little known to western botantists. Apparently it has range connections with no other species. Geographically and morphologically it is most closely related to *P. spinulosa* of the eastern Himalayas and next most closely related to Siberian spruce.

P. tianshanica Rupr. was originally applied to the material from the Thian Shan in Chinese Turkestan and was maintained as a separate closely allied species by Cheng (*in* Hu, 1934). The two species are considered synonymous by Elwes and Henry (1912) and Rehder (1940). *P. crassifolia* Komarov was described from near Lake Koko Nor in Tsinghai. Although considered by its author close to *P. shren-*

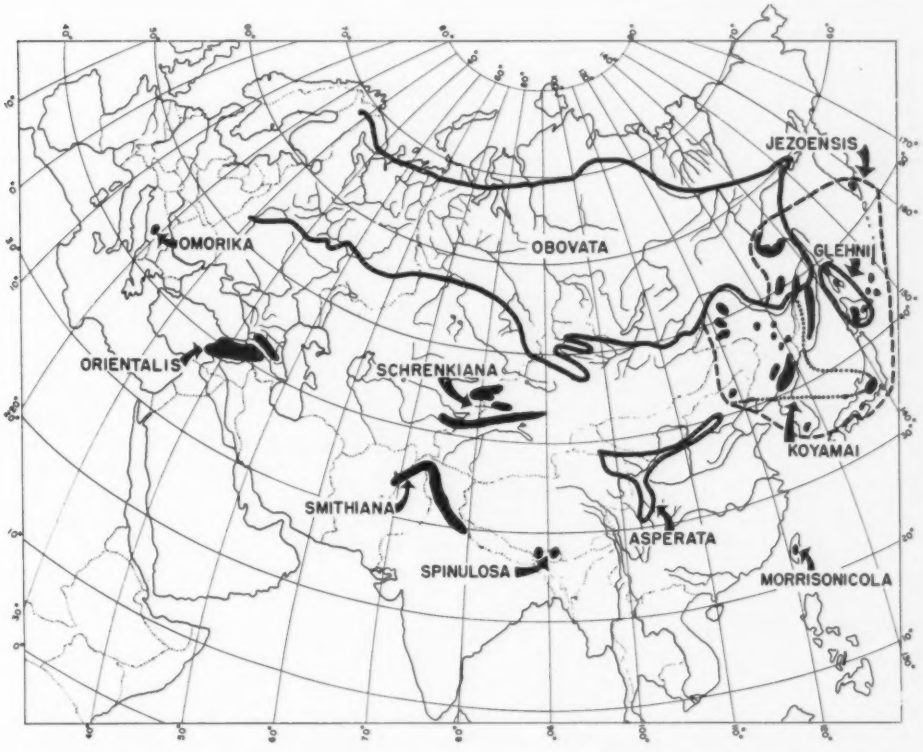

FIGURE 4. Distribution of species of Picea *in Eurasia. Species mapped in more detail in Figs. 2, 3, and 5 are omitted here. The blackened areas show the extent of actual spruce forests within the distribution limits of the species. The forests of* P. obovata *are very extensive but are probably not continuous over the entire distribution area of the species.*

kiana, it is more likely *P. asperata*, since Chinese authors mention only that species in that area.

P. SMITHIANA Boiss.— HIMALAYAN SPRUCE

This species is widespread and common in the western Himalayas, where it is an important timber tree. It is sympatric with no other species. Morphologically it is one of the most distinct species and its closest relationships are to *P. spinulosa* of the eastern Himalayas.

P. ABIES (L.) Karst.— NORWAY SPRUCE

Norway spruce is a wide-ranging species, growing from Yugoslavia to northern Scandinavia and from the Pyrenees[5] to Russia. In Yugoslavia it occurs mixed with *P. omorika*, but apparently the species do not cross. In northern Scandinavia (Lindquist, 1948) and the Upper Volga basin of Russia (Bobrov, 1944) there is a broad zone of hybridization between Norway and Siberian spruce. All recent taxonomic treatments agree that the spruce of northern Scandinavia and eastern Europe is *P. obovata* (Rehder, 1940; Elwes and Henry, 1912; and others) or *P. abies* var. *obovata* (Lindquist, 1948, and others). However, most

[5]E. J. Schreiner states in a personal communication that Spanish foresters now regard the Norway spruce in the Pyrenees as planted.

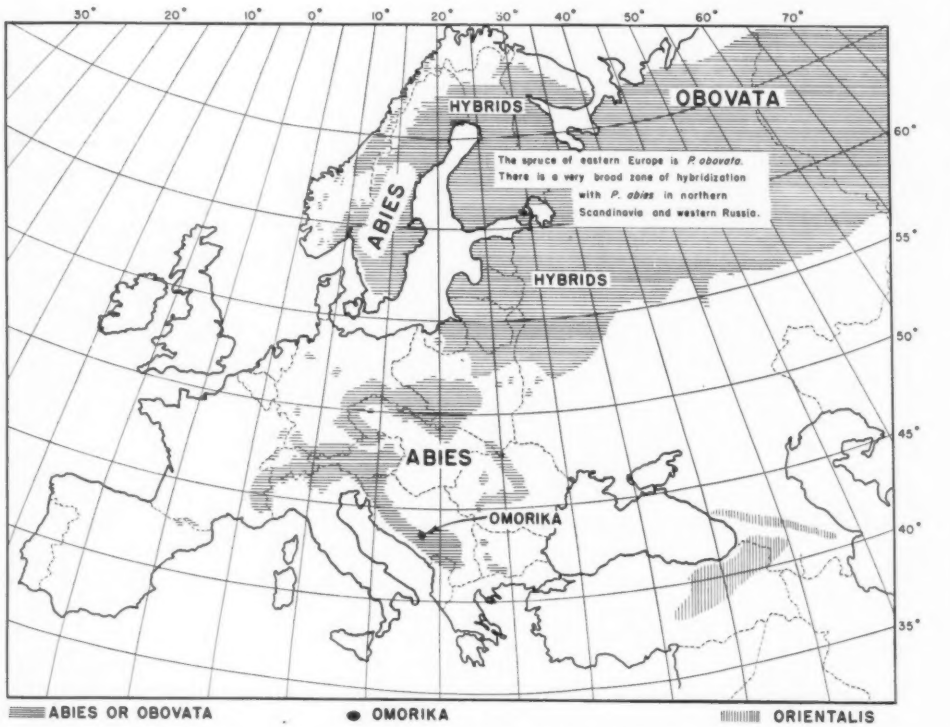

FIGURE 5. Distribution of species of Picea *in Europe. The limits of the spruce forest are drawn accurately, but no attempt is made to draw the exact boundary between* P. abies *and* P. obovata.

forestry references speak only of *P. abies* even when covering the area occupied by *P. obovata*. Evidently there are no greater growth differences between than within species. There is a great deal of racial variability within *P. abies* (Heikinheimo, 1949). Some of this is due to introgression between previously isolated populations as well as to the ordinary process of geographic differentiation.

The present Norway spruce range (Erdtman, 1933) has greatly expanded since the Pleistocene; it is still expanding. There were three major glacial refuges from which it spread; the eastern Carpathians of Rumania, the southeastern Alps, and central Russia (*P. obovata*) (Lindquist, 1948; Traunmüller, 1952). Evidences of its recent expansion are found in Finland, where there has been a noticeable expansion since the 13th century (Sauramo, 1942); in northeastern Switzerland, where it became much more common following overcutting of the original forest during the French Revolution, (Surber, 1950); and in southwest Norway, to which it has migrated in the last 1,000 years (Faegri, 1950).

P. ORIENTALIS (L.) Link.— ORIENTAL SPRUCE

Oriental spruce is endemic to the Caucasus Mountains of southern Russia and to the Turkish highlands farther south, where it is the only spruce species (Radde, 1899). It is a very important forest tree, having the largest altitudinal range (2,200 to 7,000 feet) and size (184 feet tall) of any of the conifers of the region. It commonly grows mixed with fir and beech.

P. OMORIKA (Pancic) Purkyne.— SERBIAN SPRUCE

The Serbian spruce is now endemic in a limited area (about 15 × 20 miles) in the Drina basin of southwestern Yugoslavia. Its range is entirely within that of *P. abies*, with which is frequently grows on sepentine soils at elevations of 2,600 to 5,000 feet (Fukarek, 1950). Fossils assignable to this species or to a close relative have been found in Saxony (older Quaternary), northern Prussia (Tertiary), and Czechoslovakia (Pleistocene) (Adamovic, 1909; Dyakowska, 1952). In recent historical times its stands have been decimated by fire, drought, and bark-beetles (Fukarek, 1950). According to Plavsic (1938) it is now saved from extinction only by growing on exposed sites where its narrow crown and slender trunk make it more resistant to wind than other trees.

Morphology of the Species

Table 3 was compiled from the following sources: Bulard (1946, 1947) Cheng (1939), Elwes and Henry (1906, 1912), Gaussen and Lacassagne (1930), Iwata and Kusaka (1952), Kanehira (1936), Lacassagne (1934), Martinez (1953), Melville (1950), Miyabe and Kudo (1932), Nakai (1919, 1941, 1943), Rehder (1940), Rehder and Wilson (1914), Sargent (1898, 1922), and Wilson (1916). Whenever possible, gaps in the table were filled; and differences between authors were reconciled by reference to actual plant material. This was particularly necessary for such characters as needle sharpness and curvature and color of various organs. Bark and anatomical characters are omitted because data on them are scanty.

The symbols shown in the columns of Table 3 are abbreviations for the characteristics listed at the top of the columns. For example, the first column characterizes buds as Conic, Ovoid, or Subglobose. These are abbreviated as C, O, and S in the column.

However, a separate key is used for colors (except for leaves, which are shown simply as G for green and B for blue). The colors of buds, branchlets, and mature cones are given in terms of the nearest equivalent in Maerz and Paul (1930). The colors, ranging from light down to dark, are as follows.

Buds	*Branchlets*	*Mature cones*
		Olive Sheen (light yellow-brown)
	Gray	
		Silver fern (light tan)
	Lightstone (light pink-brown)	
		Old Gold (tan)
		Tanbark algerian (tan with tinge of purple)
	Khaki	
Clay	Clay	Maple sugar (light brown)
Olive wood		Oak (dark brown)
Hazel	Hazel	Russet brown (dark brown)
	Burnt umber	
Raw umber		
Darker than raw umber		Beaver (dark purple-brown)

The colors of immature cones, female flowers, male flowers, and seeds are given simply as Red, Purple, Yellow, Green, Tan, Brown, Dark brown, and Black. All these colors are abbreviated by their capitals as shown. For example, OS is Olive Sheen, Bl is Black, and so on.

A separate key is also used for characteristics that involve measurements, such as length or organ, number of rows of stomata on leaves, and diameter of branchlets. This key is given below.

In all cases, I stands for Intermediate, and a dash (--) means that the character is not expressed. Blank spaces mean no data were available. Underlined symbols indicate that these characteristics are of the greatest diagnostic value.

For nearly all species the characterization is more complete than is given in any single manual or indeed in the original description. The table can be used in place of a key in identification work. For that purpose characters of the greatest diagnostic value have been underscored. It should be pointed out that the characterization given applies to the average for the species and that many individual characters are variable within species. It is not at all unusual to find specimens of undoubted authenticity departing from the average condition in at least two or three characters.

Table 4 was compiled by assigning each character in Table 3 a weight of 0, 1, 2, or 3 units, and then counting the number of units by which each species differs from each other species. For the 32 weighted characters studied, it would have been possible to obtain a total difference of 53 units. Each character was weighted according to

Key	Buds	Leaves	Rows of stomata Above	Rows of stomata Below	Branchlet diameter
	mm.	*mm.*	*No.*	*No.*	*mm.*
Very short	-----	6–12	2–4	2–4	1–2
Short	3–5	10–18	4–6	4–6	2
Intermediate	5–7	15–25	6–8	6–8	3
Long	7–9	20–28	8–10	8–10	4
Extremely long	8–10	25–35	10–12	10–12	5

Key	Sterigmata	Cone	Flowers	Flowers	Seed	Seed wing
	mm.	*cm.*	*mm.*	*mm.*	*mm.*	*mm.*
V	----	2–4	10–20	10–15	2–3.5	7–9
S	0.8	4–6	20–30	15–20	3.5–4.5	10–12
I	0.8–1.2	6–8	30–40	20–25	4.5–5.5	13–16
L	1.2+	8–10	40–50	25–30	5.5–6.5	17–20
E	----	10–16	----	30–40	6.5–8.0	20–24

TABLE 4. Number of characters by which spruce species differ from one another. (Compiled from Table 3. Maximum possible difference is 53.)

Species	glauca	mariana	rubens	engelmannii	pungens	chihuahuana	sitchensis	breweriana	jezoensis	glehnii	bicolor	maximowiczii	polita	morrisonicola	Koyamai	asperata	retroflexa	likiangensis	balfouriana	montigena	wilsonii	purpurea	brachytyla	complanata	spinulosa	obovata	schrenkiana	smithiana	abies	orientalis	omorika
mariana	19																														
rubens	18	7																													
engelmannii	17	22	22																												
pungens	17	22	23	12																											
chihuahuana	22	24	22	25	19																										
sitchensis	22	23	24	14	16	26																									
breweriana	23	26	23	23	24	17	23																								
jezoensis	26	28	26	14	22	29	14	26																							
glehnii	25	21	20	23	27	27	20	24	22																						
bicolor	23	26	24	26	26	23	25	21	19	23																					
maximowiczii	17	18	19	22	24	15	19	22	23	19	22																				
polita	22	26	26	22	22	12	25	26	23	26	22	18																			
morrisonicola	16	19	16	16	22	18	18	23	18	15	19	17	17																		
Koyamai	19	23	15	19	21	24	22	22	24	17	25	20	23	17																	
asperata	20	19	15	22	21	21	20	22	24	18	21	19	20	16	9																
retroflexa	24	28	25	22	19	20	17	25	24	19	21	21	21	21	12	12															
likiangensis	25	28	25	21	27	27	22	26	17	21	17	22	29	20	21	21	17														
balfouriana	23	25	20	21	23	24	22	20	24	26	16	19	25	23	15	14	15	11													
montigena	23	26	22	19	18	22	22	24	24	28	20	22	24	28	16	12	16	19	6												
wilsonii	19	21	20	15	25	18	19	23	18	24	26	19	17	14	21	26	28	25	27	27											
purpurea	22	20	18	20	28	29	20	26	20	17	21	19	26	19	21	25	24	17	18	18	16										
brachytyla	18	25	20	19	23	15	19	10	15	20	20	19	18	13	19	20	25	24	24	23	15	21									
complanata	22	27	23	19	23	17	21	15	16	19	17	17	16	12	24	25	24	22	23	26	17	23	8								
spinulosa	18	21	19	18	16	20	14	18	19	22	23	21	16	16	19	20	19	19	23	24	17	23	16	17							
obovata	15	23	19	22	26	21	24	18	25	22	21	19	23	14	20	20	23	18	19	23	20	19	17	19	21						
schrenkiana	22	24	21	25	21	27	20	22	29	27	31	23	21	19	23	23	19	24	29	30	20	30	22	23	13	18					
smithiana	23	30	26	26	29	24	23	29	24	26	22	16	21	22	24	25	26	23	22	25	26	28	24	23	17	21	23				
abies	17	22	19	18	16	20	24	21	26	26	17	22	25	18	14	15	16	18	14	15	25	25	21	24	18	18	23	24			
orientalis	23	22	16	22	25	19	25	18	26	20	22	11	17	16	17	18	23	21	16	17	19	16	19	18	22	14	20	23	23		
omorika	25	17	13	19	24	28	24	21	20	20	27	22	29	16	23	24	29	22	24	28	22	16	20	20	21	20	26	31	25	21	

the ease and accuracy with which different degrees of the character could be recognized. For example, cone length was given a weight of 3 and acuteness of terminal bud a weight of 1 because it is possible to recognize differences in cone length much more easily than it is to recognize degrees of terminal-bud acuteness. A weight of 0 was given characters for which data were lacking for several species. For the little known species *P. morrisonicola*, *P. schrenkiana*, *P. spinulosa*, and *P. chihuahuana* it was necessary to extrapolate to account for some missing character descriptions.

In the computation of Table 4 the characters were given the following weights:

Weight of 0: Characters 20–24, 34, 38–46, 48–51.

Weight of 1: Characters 2, 7, 10, 14–17, 26–28, 32–33, 37, 47.

Weight of 2: Characters 1, 3–6, 8–9, 12–13, 18, 25, 29–31.

Weight of 3: Characters 11, 19, 35–36.

Figure 6 was drawn by arranging the species in their approximate geographic positions and connecting them with lines of varying thickness according to the number of differences indicated in Table 4. Species differing by 18 or more units are left unconnected. This diagram only approximates a phylogenetic chart because parallel evolution or chance may be responsible for some of the seemingly strong relationships. Nevertheless, the fact that most lines connect neighboring species between which there are probable migration routes indicates that degree of morphological similarity does have great phylogenetic significance. In a later section the morphological, genetic, and distribution data are combined to give probable phylogenetic trends.

Evolution and Phylogeny of Spruce

The relation between distribution, morphology, and species crossability is shown in Table 5. Of 70 attempted crosses, 16 were apparently successful, 12 were doubtfully successful or successful only a portion of the time, and 42 were unsuccessful. Of the 16 apparently successful crosses, 14 involved species that were morphologically similar or had neighboring ranges or both.

TABLE 5. Relationships between species crossability, geographic distribution, and comparative morphology.[1]

Successful crosses	Unsuccessful crosses
MORPHOLOGICALLY SIMILAR SPECIES WITH GREATLY OVERLAPPING RANGES	
mariana × *rubens*	
MORPHOLOGICALLY SIMILAR SPECIES WITH SLIGHTLY OVERLAPPING OR NEIGHBORING RANGES	
engelmannii × *glauca, sitchensis* *asperata* × *montigena, retroflexa*[2] *retroflexa* × *montigena, balfouriana, koyamai* *abies* × *obovata*	*obovata* × *orientalis*
MORPHOLOGICALLY SIMILAR SPECIES WITH WIDELY SEPARATED RANGES THAT ARE CONNECTED BY AN INTERMEDIATE SPECIES	
montigena × *koyamai, abies* *abies* × *asperata, koyamai*	*abies* × *retroflexa* *sitchensis* × *pungens*
MORPHOLOGICALLY DISTINCT SPECIES WITH GREATLY OVERLAPPING RANGES	
jezoensis × *glehnii*[2] *mariana* × *glauca*[2]	*abies* × *omorika* *glauca* × *rubens*
MORPHOLOGICALLY DISTINCT SPECIES WITH NEIGHBORING RANGES	
orientalis × *omorika*,[2] *abies* *mariana* × *jezoensis*[2] *asperata* × *obovata*	
MORPHOLOGICALLY DISTINCT SPECIES WITH NEIGHBORING RANGES AND A COMMON ANCESTOR	
glauca × *jezoensis, sitchensis*	
MORPHOLOGICALLY DISTINCT SPECIES WITH WIDELY SEPARATED RANGES	
omorika × *koyamai, sitchensis*[2] *glauca* × *asperata, koyamai* *abies* × *mariana, rubens, siltchensis*	*glauca* × *wilsonii, maximowiczii balfouriana, retroflexa, montigena, abies, omorika, orientalis* *mariana* × *maximowiczii, balfouriana, retroflexa, montigena, asperata, obovata* *engelmannii* × *abies, maximowiczii, retroflexa, montigena, asperata, omorika, orientalis* *sitchensis* × *asperata* *jezoensis* × *orientalis, montigena, retroflexa* *maximowiczii* × *abies, asperata, montigena* *orientalis* × *asperata, montigena, pungens* *omorika* × *asperata, montigena, obovata, wilsonii, balfouriana, breweriana*

[1]Morphologically distinct species are those not connected by lines in Figure 6. Only the crosses that have been tried (see Table 2) are listed. Direction of cross not shown by order of listing.

[2]These crosses were doubtfully successful in only a part of the tree × tree combinations, or the hybrids are rare in nature.

Of the 42 failures, 37 involved morphologically distinct species with widely separated ranges.

In the two following sections the morphology, distribution, and genetic data are brought together to form a coherent picture of the evolution and phylogeny of the genus as a whole. The first section contains postulates on the pattern that evolution has followed in spruce. The second section is a summary of phylogenetic trends. The conclusions are strongest where all three lines of evidence agree. No conclusions are possible where all three lines of evidence disagree or where data from only one line of evidence are available.

It would be desirable to include the fossil history of the genus as a fourth line of evidence. However, the fossil history (La Motte, 1952) is fragmentary. Most of the Pleistocene and Recent fossils were found near or within the ranges of the living species to which they are referable. There are too few good fossils from earlier periods to help much in completing the phylogeny.

Spruce Evolution Patterns

Following are listed a series of postulates (in *italics*) and supporting proof on the patterns of evolution in the spruces.

1. *Picea had a monophyletic origin.*

There are no sharp breaks within the genus that indicate a polyphyletic origin. Even the most distantly related spruce species seem much more similar to each other than any one of them is to a species of another genus. For example *Picea* and *Tsuga* are considered closely related genera. Yet there is no overlapping between these genera in a great many characters, including the following: number of resin canals per needle, shape of needle tip, number of scales per cone, number of anthers per male flower, position of the stomata, pollen grain wings, and variation in needle length.

2. *The basic spruce type has been changed relatively little in becoming differentiated into the present array of species. In genetic terms, mutations have occurred at many loci, but relatively few allelomor-*

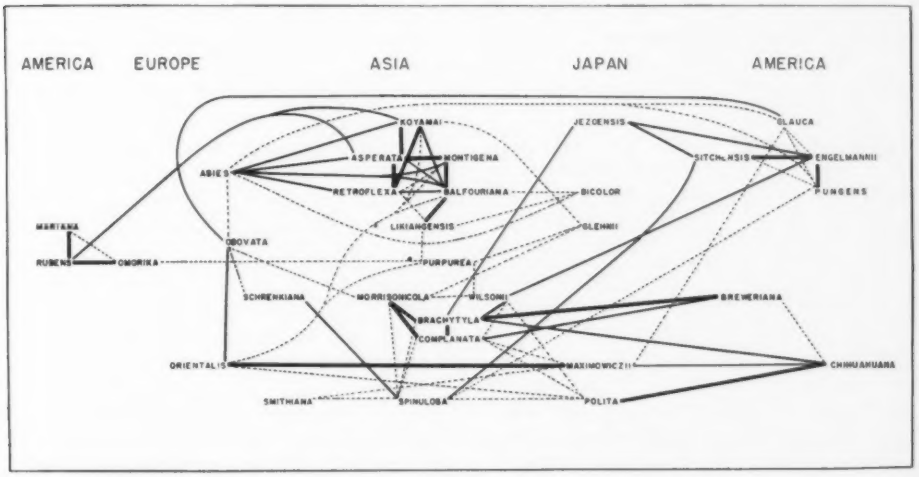

FIGURE 6. Taxonomic relationships between species of Picea. *Except for* P. obovata *and* P. morrisonicola, *which grow in Siberia and Formosa respectively, the species are arranged according to their approximate relative geographic positions. The heavy, light, and dotted lines indicate respectively less than 13, 14–15, and 16–17 differences between the species. As noted in the text, this chart only approximates a phylogenetic chart.*

phic genes have been produced at any one locus. Moreover, the interactions between genes have been weak and no trends involving many genes have become established.

Although there are many variable characters in spruce, the range of variation in any one character is small, and each character may be associated with almost any combination of other characters. Taxonomically the genus is more nearly comparable to a single series in pine, maple, or ash than to any one of these complete genera. The author has found it as difficult to identify species of spruce as to identify ecotypes of white ash.

The genus is also more uniform in wood anatomy, growth, and ecology than these other large genera. Although a few of the species have distinctive woods, most of them are so similar in wood properties that they are not separated in harvesting and marketing. All the species have medium-wide to narrow, pointed crowns, and (except for *P. sitchensis*) all are found at either high latitudes or high altitudes. Most of the species occupy mesophytic sites; black and Yeddo spruce also occupy swamps. In order to maintain approximately the same temperature and moisture condition for the seedlings there has been some differentiation with regard to position in succession; the high altitude southern species are in general more tolerant than the northern species.

We can often trace the migration route of a single character through two or three adjacent species, but almost always this same character crops up again in a distant species against a different genetic background. There are so many cases of this parallel evolution as to indicate that most of these characters are controlled by relatively few genes.

The excellent crossability between adjacent species or between species connected by intermediates also indicates that the total amount of genetic differentiation has been slight. So far *P. maximowiczii* is the only species used to any extent that has not been crossed with at least one other species.

Just why the spruces should have differentiated so little is still a matter for conjecture. Presumably selection pressure operates on spruce as on other genera. It would require extremely low mutation rates (probably not more than 1/100 of those found in other genera) to explain the

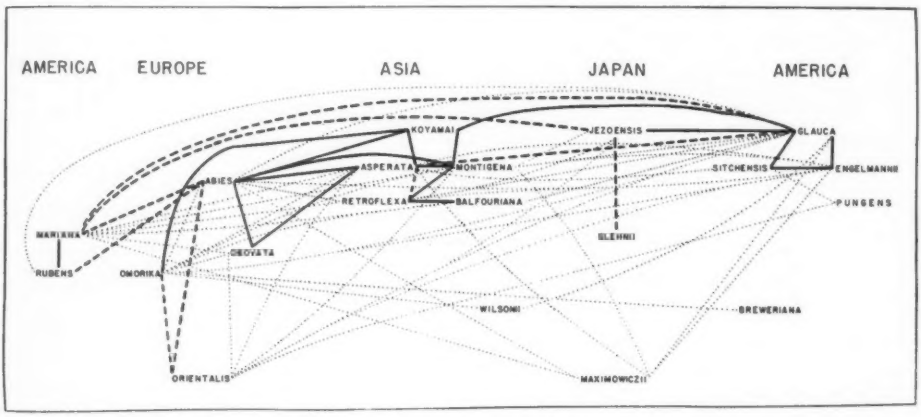

FIGURE 7. Successful (solid line), moderately successful (dashed line), and unsuccessful (dotted line) species crosses in the genus Picea. *The species are arranged as in Figure 6. Relative success of all crosses determined from comparative seed sets. Most of the successful crosses involve species with similar morphology or neighboring ranges.*

lack of variability. Perhaps there is something inherent in the spruce germ plasm that resists change. Kiellander's (1950) finding that polyploidy results in dwarfness (lethal in nature) supports this view.

3. *The genus originated in northeast Asia, whence it spread by migration across boreal routes and southward along mountain chains.*

Li (1953) believes that nearly all coniferous genera arose around the edge of the Pacific Basin because all are represented there whether or not they are represented around the Atlantic Basin. This indicates either eastern Asia or western America as the probable center of origin for spruce. Of these two regions, eastern Asia seems the logical choice because it contains the largest assortment of species and also contains *P. koyamai*, a likely choice for the most primitive species.

The Japanese island of Honshu contains five species that are so distinct that they could hardly have become differentiated within the area of Japan. They are best regarded as migrants from other places of origin. For this reason the mainland of Asia is the most likely center of origin for the genus.

At the present time there is actual continuity of the spruce forest over most parts of boreal America and Eurasia. While the Alaska-Kamtchatka range gap is large, it has evidently been open to spruce migration in relatively recent times (see *P. jezoensis*) and is still open to arctic plants. We need postulate relatively minor fluctuations in climate to explain southward migration along known mountain migration routes for nearly all modern southern species. On the other hand, we should need to postulate great climatic changes as well as nonexistent mountain chains and land bridges to explain east-west migration along purely southern routes.

4. *The southern species, in comparison with the northern species, have smaller ranges, many of which are decreasing at the present time. Genetic uniformity and specialization for survival in southern habitats, but with less capability for evolutionary change than the associated competing angiosperms, have contributed to the range diminution.*

In this discussion southern and northern species are defined according to relative geographic positions on their respective north-south migration routes rather than on absolute latitudinal ranges or absolute temperature requirements.

In every region, the more southern species have the following characteristics that distinguish them from their northern neighbors:

Greater taxonomic uniformity. In each of the most northern species (*P. glauca, P. mariana, P. engelmannii, P. sitchensis, P. jezoensis, P. koyamai, P. asperata, P. obovata*, and *P. abies*) there are recognized geographic races, taxonomic varieties, or taxonomic mixups indicating genetic diversity. In contrast, almost all the name changes that have occurred in the southern species have involved questions of priority or genus limits (many species were described originally as pines).

More isolation. Six southern species (*P. orientalis, P. smithiana, P. spinulosa, P. morrisonicola, P. breweriana*, and *P. chihuahuana*) are isolated from any other spruce species by 1,000 miles or more. Several others are in geographic contact only with species with which they probably do not cross. In contrast, each of the northern species mentioned in the preceding paragraph is now or could have been in recent geographic and genetic contact with one, two, or three other species.

Larger maximum size, good growth vigor, and relative freedom from pests. In their native habitats nearly all the southern species grow to greater maximum sizes than do their nearest boreal neighbors (see Table 3). Only in western America is this relationship reversed (*P. sitchensis* grows taller than does *P. breweriana*). Available literature accounts mention no serious pests of the mature trees that could explain the

smallness of the ranges. There are few data on seeding habits of the species in their native habitats; in Philadelphia three southern species (*P. rubens*, *P. orientalis*, *P. omorika*) seeded well after adequate pollination.

Greater tolerance and tendency to grow in remote mountain areas. In moving south the southern species have moved to higher altitudes and taken advantage of the shelter offered by other plants in order that they could live in approximately the same temperature and moisture regime as their northern neighbors. Such northern species as *P. galuca*, *P. engelmannii*, *P. asperata*, *P. obovata*, and *P. abies* characteristically occur in pioneer communities composed of relatively few species. Such southern species as *P. rubens*, *P. breweriana*, *P. wilsonii*, *P. purpurea*, *P. orientalis*, and *P. omorika* characteristically occur in communities that are nearer the climax and are composed of a larger number of species. Several southern species (*P. pungens*, *P. chihuahuana*, *P. breweriana*, *P. morrisonicola*, . *maximowiczii*, *P. wilsonii*, *P. spinulosa*, and *P. omorika*) are little exploited because of their remoteness from civilization.

Smaller ranges, which may be shrinking at the present time. Seven southern species (*P. omorika*, *P. spinulosa*, *P. maximowiczii*, *P. bicolor*, *P. morrisonicola*, and *P. chihuahuana*) have ranges of only a few square miles each. In western China *P. purpurea* and *P. wilsonii* are losing ground whereas the more northern *P. asperata* is increasing its range (Teng, 1947a); in eastern America *P. rubens* is losing ground whereas *P. glauca* is increasing its range (Westveld);[6] in Yugoslavia the proportion of *P. omorika* in mixed *P. omorika-P. abies* stands is decreasing (Plavsic, 1938). *P. breweriana* (Elwes and Henry, 1906) and *P. rubens* are difficult to raise from seed in nurseries. Of the five species that have been used to any extent in forest plantings outside their native ranges (*P. glauca*, *P. sitchensis*, *P. abies*, *P. koyamai*, and *P. omorika*) only *P. omorika* is a southern species. These facts indicate that the shrinking ranges are at least partly due to inherent characteristics of the species.

Genetic uniformity is probably one of the reasons for the lack of success of the southern species. Isolation and small population size are probably the most important reasons for this genetic uniformity. In seven southern species the total population size is small enough to lead to uniformity through inbreeding. In others the total population is relatively large but is broken up into small subpopulations. If these small subpopulations could occasionally coalesce, this situation would lead to increased variability. However, in such a species as red spruce many of the stands situated near mountaintops would be exterminated and a great part of the total species variability would be destroyed during a warm period.

The spruces (or for that matter all gymnosperms) seem to have had slower evolutionary rates of change than angiosperms. Hence, specialization for reproduction in a southern near-climax habitat composed largely of angiosperms would have put the southern spruces at an evolutionary disadvantage.

5. *The isolating mechanism involved in speciation has usually been geographic rather than internal. Only after species have been separated for considerable periods is there enough genic differentiation to prevent crossing. The removal of geographic barriers has often resulted in the production of hybrids, and introgression may have played a significant role in the evolution of many of the species.*

There are three different types of isolating factors that have been responsible for speciation in the spruces: geographic isolation, differences in flowering time, and other internal genetic factors.

The fact that most morphologically similar species with allopatric but neighboring ranges cross with each other indicates that geographic isolation has been the pri-

[6]Personal communication.

mary factor in most cases, and that internal factors did not become operative until the species had been geographically isolated for long periods of time. At least in the Philadelphia area, all trees of the same species have similar enough flowering times that they can cross with each other. This being so, it is reasonable to assume that the differences in flowering time between different species arose as a consequence of the geographic isolation and were not in themselves the primary isolating factor.

In most regions where two or more species are sympatric over large areas, the species are morphologically dissimilar to each other and probably originated elsewhere than in their present ranges. This is especially true of the Japanese species. Each of these is more closely related morphologically to a species of the Asiatic mainland than to another Japanese species. These facts make it unreasonable to assume that these Japanese species all originated on Japan because of internal isolating factors.

In eastern Europe (Bobrov, 1944), Alaska and southern British Columbia (Little, 1953a), Denmark (Thaarup, 1945), northern New England (Heimburger, 1939), and probably in western China, natural hybridization is common. In the cases of Siberian × Norway and of white × Engelmann spruces this hybridization appears to have led to introgression.

Phylogenies of Species Groups

The present phylogenetic scheme, based on a consideration of distributional and genetic data as well as on 32 morphological characters, does not attempt to place in their proper positions several incompletely known species, and recognizes no section lines. In these respects it differs from the schemes used by Lacassagne (1934) and Rehder (1940).

There is no natural break in the genus sufficient to warrant the erection of section lines (Fig. 6 and Fig. 7).

There are sufficient data to allow us to sketch probable phylogenies for several groups of species if not for the genus as a whole. The principal groups are summarized below.

P. rubens-mariana group of eastern America. Distributional and morphological evidence indicates a close relationship between these species. They are probably remnants of a more ancient migration than that which gave rise to the species of northwest America.

Northwest America group (*P. glauca, P. engelmannii, P. pungens, P. sitchensis*). Morphological, distributional, and genetic data indicate a common, relatively recent origin for all these species; they are probably related to the Old World species through *P. jezoensis* of Japan. *P. breweriana* and *P. chihuahuana* are morphologically most similar to some of the south Asiatic species. They are almost certainly of different stock than the other species of northwest America.

Japanese species. The morpholocial evidence indicates that the six Japanese species have six different origins. This view is borne out by the fact that they live sympatrically without apparent crossing, and have probably done so for thousands of years. *P. koyamai* has already been mentioned as possibly being the oldest type in the genus, and is almost certainly closely related to the spruces of north China and to Norway spruce. *P. jezoensis* finds its closest mainland relatives in the *P. brachytyla* complex and is the probable intermediate to the species of northwest America. Each of the other species is most similar to different south Chinese species.

Southwestern Chinese and Formosan species (*P. brachytyla, P. purpurea, P. wilsonii, P. morrisonicola*). The morphological and distrbutional evidence indicates a common origin for all four species. However, the fact that the three Chinese species can live sympatrically and remain distinct indicates that this common origin is relatively ancient.

Himalayan species. The morphological and distributional evidence indicates that *P. spinulosa* was probably derived from

south Chinese stock, and that it in turn gave rise to the western Himalayan *P. smithiana*.

North Eurasian and north Chinese species. Morphological and crossing data indicate that *P. abies*, *P. koyamai*, the *P. asperata* complex and the *P. likiangensis* complex form a closely related group with a relatively recent common origin. Morphologically *P. obovata* does not fit into this group and does not seem to be the parent of Norway spruce as the distribution and crossing data indicate.

P. orientalis. Distributional, morphological, and crossing evidence agree in showing that this species is related to Norway, Serbian, and Siberian spruces. However, its exact relationship to these three species is not clear.

Summary

The results of 6 years' artificial-pollination experiments in the spruces are presented. Including the results of other workers, 70 different interspecific combinations (not including reciprocals) have been attempted. Most of the unsuccessful crosses were repeated two or three times; the successful crosses were usually repeated more. Of the 70 different combinations attempted, 16 were judged successful on the basis of consistently high sets of filled seeds, 12 were doubtfully successful or were successful in only a small portion of the time, and 42 were unsuccessful. Of the 16 apparently successful crosses, 14 involved species that were morphologically similar or had neighboring ranges or both. Of the 42 failures, 37 involved morphologically distinct species with widely separated ranges.

No growth data are included in this paper, but mention is made of those hybrids whose hybridity has been authenticated in nursery or plantation tests.

Detailed range maps of all recognized species are given. As far as the scales of the maps permit they are accurate except for the species found in Siberia and central and southern Asia. The comparative morphology of all species is given in tabular form. From those data the taxonomic relationships between species were deducted by computing the number of characters by which every species differs from every other species. This method indicates that previously recognized sections are artificial.

The distributional, genetic, and morphological data are all used to formulate hypotheses on the evolution of the genus. All three lines of evidence agree in indicating that four species of northwestern America are closely related to each other and to a Japanese species; that red and black spruce of eastern America are closely related; that Norway spruce and certain species of Manchuria and North China are closely related; that some of the south Chinese species are closely related; and that the Japanese species are not closely related to each other although each is closely related to certain Chinese species. In other cases where the three lines of evidence disagree, phylogenetic trends are less clear.

Several facts indicate that the genus had its origin in northeast Asia, whence it radiated in more than one wave of migration. Crossability barriers seem to have arisen mainly from genic differentiation following sufficient geographic isolation. Rarely has isolation just long enough to produce a new species resulted in sufficient lack of crossability to preclude hybridization if the geographic barrier was subsequently removed. Introgression is observable in two different regions now and has probably played a significant role in the past.

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